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The palaeobiology of the bivalve families Pectinidae and Propeamussiidae in the Jurassic of Europe

by
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with 213 text figures, 11 plates,
4 tables and 2 appendices

ABSTRACT

This work deals systematically with all the pectinids and propeamussiids that occur in the Jurassic of Europe apart from the genus *Weyla* and a suite of distinctive species largely confined to the Tithonian of Alpine and southern Europe. By applying a species concept in which all members of an evolving lineage are accorded the same specific name, 34 species are recognised (3 in the genus *Propeamussium*, 3 in the genus *Entolium*, 4 in the genus *Pseudopecten*, 5 in the genus *Spondylopecten*, 6 in the genus *Camptonectes*, 3 in the genus *Eopecten*, 3 in the genus *Chlamys* and 7 in the genus *Radulopecten*). Each species is described, with the aid of biometric information, and its taxonomy is discussed in detail. Following this, stratigraphic and geographic range is described, the latter with the aid of maps (including pre-drift reconstructions for extra-European distribution). Sedimentary and faunal associations are set out and from this information an attempt is made to reconstruct palaeosynecology. Mode of life is inferred both by means of drawing analogies with living, morphologically similar species and through comparison with sets of morphological "paradigms" deduced for the various modes of life of scallops. In the section introducing the "paradigms" special attention is given to the likely function of shell plication. A concluding section for each species discusses origins and the rate and possible genetic basis of any phyletic changes.

KURZFASSUNG

Alle Pectiniden und Propeamussiiden, die im europäischen Jura vorkommen, werden in diesem Werk systematisch behandelt, abgesehen von einer Reihe besonderer Arten, die hauptsächlich im Tithon des alpinen und südeuropäischen Raumes vorkommen. Durch Verwendung eines Artbegriffes, wobei alle Mitglieder einer Abstammung als eine Art betrachtet werden, können 34 Arten anerkannt werden (3 in der Gattung *Propeamussium*, 3 in der Gattung *Entolium*, 4 in der Gattung *Pseudopecten*, 5 in der Gattung *Spondylopecten*, 6 in der Gattung *Camptonectes*, 3 in der Gattung *Eopecten*, 3 in der Gattung *Chlamys*, 7 in der Gattung *Radulopecten*). Jede Art wird beschrieben (mit Hilfe biometrischer Daten), und taxonomische Fragen werden gründlich diskutiert. Danach werden die stratigraphische und geographische Verbreitung diskutiert, im letzten Fall mit Hilfe von Karten (einschließlich paläokontinentaler Zusammenstellungen für Daten außerhalb Europas). Sedimentologische und faunistische Beziehungen werden beschrieben, worauf versucht wird, ein Bild der Paläosynökologie zusammenzustellen. Auf die Lebensweise wird nicht nur durch Analogie mit lebenden, morphologisch ähnlichen Formen geschlossen, sondern auch durch einen Vergleich mit ,,Paradigmen", die für jede der verschiedenen Lebensweisen bei Kammuscheln abgeleitet werden. In der Entwicklung von ,,Paradigmen" wird die Rolle der Berippung bei Kammuscheln besonders berücksichtigt. Für jede Art wird in einem zusammenfassenden Abschnitt der Ursprung, die Geschwindigkeit und die vermutliche genetische Basis für phyletische Veränderungen diskutiert.

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CONTENTS

I. INTRODUCTION

The present work is in essence a somewhat condensed version of the author's doctoral thesis 'The palaeobiology of the bivalve family Pectinidae in the Jurassic of Europe' (Johnson, 1980). The Propeamussiidae were also included in the latter work, the word Pectinidae being interpreted sensu lato to mean all scallops. The original research was undertaken with a view to providing data for the then nascent debate over the tempo and mode of evolution (review in Gould and Eldredge, 1977) and it is hoped to discuss the evolutionary implications of the data presented herein in a future publication.

In the course of the research the author undertook extensive field work in England (supplemented by studies in France and Germany) and examined museum material preserved in some 18 institutions spread through England, France and Germany. To all those who helped by making collections available for study and to the many others who assisted in the research (financed from the Burdett-Coutts Fund, University of Oxford) grateful thanks are offered. A full list of acknowledgements is presented in the author's thesis. Latterly, Mrs. V. Jenkins has been of the greatest assistance in typing corrections to the final draught of the manuscript.

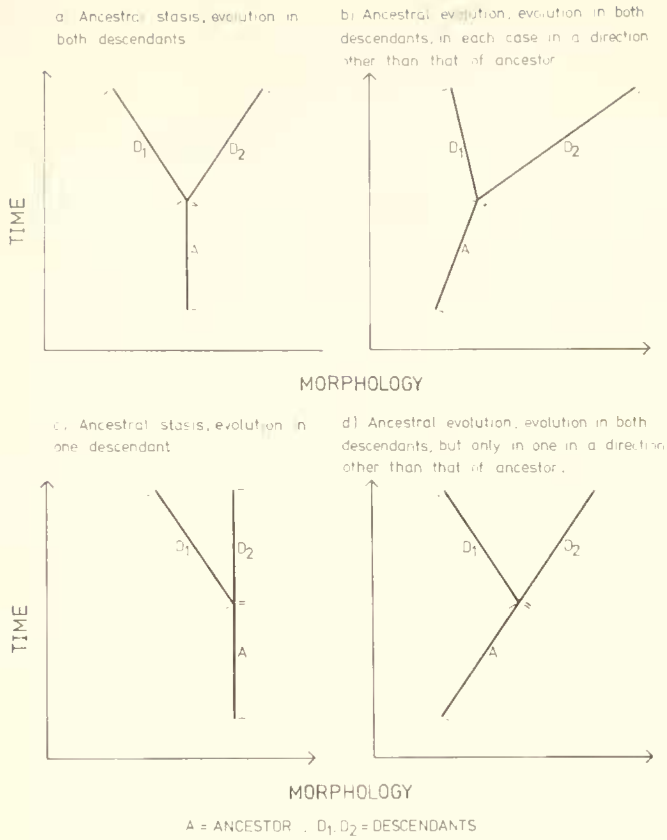
The original study was succeeded by an investigation of the Upper Triassic and Lower Jurassic bivalves of alpine Europe. Relevant information from the latter research, financed by the Alexander-von-Humboldt-Stiftung and carried out at the Universitäts-Institut für Paläontologie und historische Geologie, München (where the author's collection is now housed), has been incorporated herein.

It proved impossible to gain more than a very superficial picture of the palaeobiology of a suite of distinctive species largely confined to the Tithonian of southern and alpine Europe. These species (for which d'Orbigny's (1850) name *Pecten Insularum*, Gemmellaro and Di Blasi's (1874) names *P. nebrodensis*, *P. oppeli*, *P. billiemensis*, *P. siculus*, *P. polyzonites*, *P. acrorysus*, *P. poecilographus*, *P. zitteli* and *P. grammoproticus*, Boehm's (1883) names *P. clare rugatus* and *P. fraudator* and Blaschke's (1911) name *P. polycyclus* are available) are excluded from formal treatment herein. The genus *Weyla*, which occurs in Europe but is far more abundant in the Americas (Damborenea and Manceñido, 1979) is also excluded. Data on the extra-European distribution of the formally analysed species has however been included in order to present a more complete picture of the palaeobiology of these species.

Mode of life was judged in some cases by drawing analogies with living, morphologically similar forms. However, in an attempt to introduce more rigour into the analysis, a variant of the 'paradigm' approach (Rudwick, 1964) was also employed. The methodology here is comparison of the given shell morphology with sets of ideal dimensions and qualities (the paradigms – presented in Part II) devised for the various modes of life.

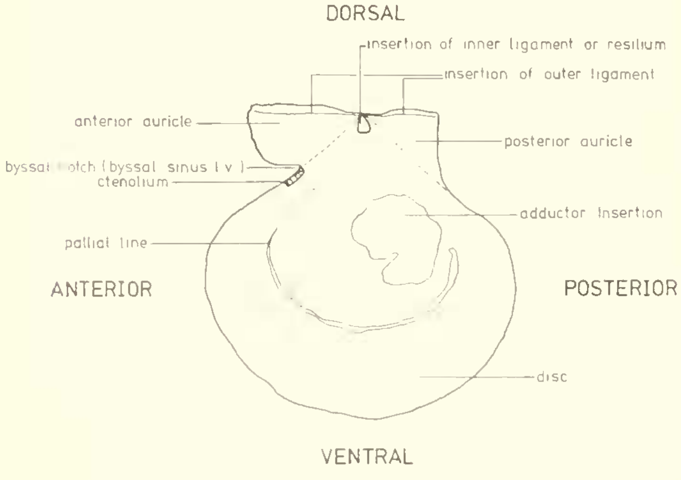
SPECIES CONCEPT

If significant morphological evolution occurs in some fraction of a species' total population or if it occurs throughout a species' total population in two or more different directions we have speciation, in the multiplicative sense of the word. Significant morphological evolution in the same direction throughout a species' total population (phyletic evolution) is speciation in the non-multiplicative sense of the word. A number of notable modern authors (e. g. Gould and Eldredge, 1977: 119; Stanley, 1978: 27, 28) have restricted their use of the term speciation to the multiplicative process in order to simplify discussion of the relative importance of this and the non-multiplicative mode of evolution. Since such discussion was one of the author's research objectives (see above) the 'modern' approach has been followed herein. It has the effect that separate specific names can only be applied to the separate branches emanating from a branching point in a phylogenetic tree (i. e. the branches themselves cannot be subdivided into separate species even if they signify considerable phyletic evolution). Whether all of the two or more descendant branches should be accorded different specific names must be decided by whether they can all be thought of as constituting fresh branches. This in turn must be decided by the mode of arrangement of the branches in the case in question. Four basic configurations can be envisaged (text fig. 1). In a) and b) it is clear that both D_1 and D_2 should be accorded a different specific name to A while in c) it is correspondingly clear that D_2 must be accorded the same specific name as A. The latter is also the most logical solution to d) although it is less easy to perceive D_2 and A as parts of the same branch. In practice, of course, only segments of the branches of a phylogenetic tree are known. Where such segments overlap temporally it is clear that they must be accorded separate specific names. In the case of stratigraphically separated but obviously related segments one can only guess whether they

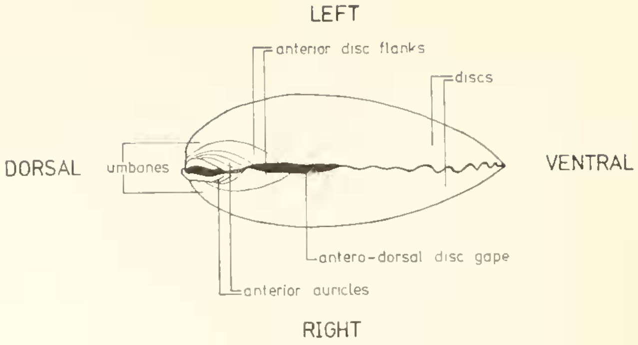


Text fig. 1: The four basic potential branch configurations about a simple bifurcation in a phylogenetic tree.

constitute parts of the same branch and should therefore be accorded the same specific name, or whether they constitute parts of different branches and should therefore be accorded separate specific names. Thus in such cases application of the 'modern' species concept defeats the object for which it was originally introduced, that of clearly differentiating multiplicative from non-multiplicative processes of evolution. If such cases are common one might just as well employ a 'traditional' species concept. The author came across relatively few instances where an arbitrary decision had to be made and therefore feels justified in having employed the 'modern' concept.



Text fig. 2: Simplified interior view of the right valve of the extant pectinid *Gloripallium pallium;* l. v. = left valve (adapted from WALLER, 1972b: 228).



Text fig. 3: Simplified anterior view of the extant pectinid *Argopecten purpuratus* (adapted from WALLER, 1969: 9).

GENERAL FEATURES AND DESCRIPTIVE TERMINOLOGY

Text figs. 2 and 3 illustrate major features of typical pectinids and serve to introduce most of the potentially unfamiliar morphological terms employed herein. A few of the terms appear to have been invented by WALLER (1969) but most have a long history of usage. Orientation is conventional rather than anatomical with an imaginary line meeting the outer ligament perpendicularly at the resilium marking the boundary between the anterior and posterior shell sectors and an imaginary line perpendicular to the latter halfway between the resilium and the ventral margin marking the boundary between the dorsal and ventral shell sectors.

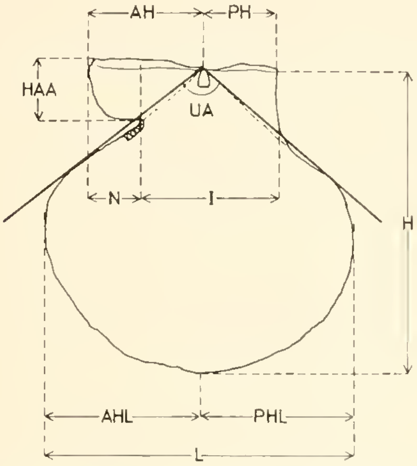
The outline of the left disc is almost always a mirror image of the right. The auricles of the left valve are, however, never extended more than fractionally dorsal of the outer ligament insertion (at least in post-Palaeozoic forms) while those of the right valve are usually at least noticeably (sometimes very markedly) extended beyond the outer ligament insertion. The base of the anterior auricle of the left valve is, moreover, rarely excavated to the same extent as that of the right valve.

The terms byssal notch and byssal sinus, referring respectively to excavations at the bases of the right and left anterior auricles, derive from the fact that the byssus (if any) is extended out of the shell (via the comb-like structure known as the ctenolium) in the area immediately ventral to the anterior auricles.

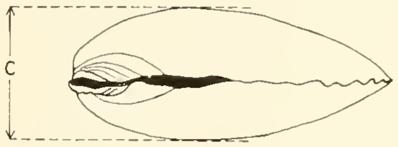
The terms equivalve/inequivalve and equilateral/inequilateral are used herein only with reference to that great majority of the shell constituted by the discs. Practically all scallops (i. e. pectinids and propeamussiids) have to be regarded as inequivalve and inequilateral if the auricles are included into consideration (see above).

Most of the terms such as lamellae, spines, tubercles used herein to describe ornament need no clarification. A few words are however called for in connection with the terms plicae, costae, striae and sulci. The term plicae is applied to radial corrugations affecting the entire thickness of the shell at the ventral margin. All other forms of radial ornament are termed costae except where very fine (relief less than about 0.1 mm), in which case the term striae is used. Sulci are the troughs between plicae and costae.

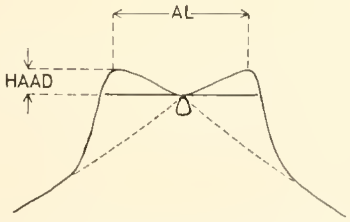
The terms original and initial are applied to the first formed or primary plicae, costae or striae in species which have secondary plicae, costae or striae (as a result either of intercalation or splitting). The term original is used where the first formed plicae, costae or striae in fact appear at the start of post-larval ontogeny and the term initial is used where the first-formed plicae, costae or striae appear somewhat later.



Text fig. 4: General dimensions measured in this study: 1. In the plane of commissure (based on the specimen illustrated in text fig. 2; all parameters apart from N are also measurable in the left valve).



Text fig. 5: General dimensions measured in this study: 2. Perpendicular to the plane of commissure (based on the specimen illustrated in text fig. 3).



Text fig. 6: Special dimensions: measurable only in *Propeamussium (P.) laeviradiatum* and species of *Entolium* (based on a generalised *Entolium* right valve umbonal region, seen from the inside).

MORPHOMETRY AND METHODS OF COMPARISON

In an attempt to make the study more rigorous it was decided to back up the tried and tested 'eyeball' method of comparison with quantitative methods. To this end some 4000 specimens, representing perhaps half of the total numer examined, were measured in up to 15 parameters (usually about 6 or 7). Non-ornamental parameters are illustrated, together with the abbreviated names given to them for the purposes of easy graphing, in text-figs. 4–6. Their full names are listed in Table 1 together with clarificatory notes where necessary. All linear dimensions are measured either perpendicular or parallel to the hinge line. Ornamental parameters measured, where possible, include the number of plicae (PL), the number of external costae (EC) and the number of internal costae (IC). These need to clarification except in so far as it is necessary to say that folds merging into the disk flanks were not counted as plicae.

Linear dimensions were measured with vernier callipers. In equivalve species the parameter C was in some cases ascertained by measuring the convexity of a single valve and then doubling. The parameter UA was measured with a contact goniometer. It is technically rather difficult to measure UA accurately with a contact goniometer in species where the umbo projects beyond the hinge line and in small specimens of all species. In the latter case 'measuring error' is probably random but in the former it is likely that the actual values are systematically underestimated, the tendency to underestimate probably increasing with increasing umbonal projection. Measuring error is otherwise probably between 1 and 2° for UA and about 0.2 mm for linear measurements.

Analysis of the quantitative data was restricted to the plotting of bivariate graphs and histograms.

PRESENTATION OF RESULTS

A standard systematic format has been used. No attempt at a complete revision of the supra-specific classification has been made since for many groups this would require a considerable knowledge of forms occurring outside the Jurassic. At the generic level the author has followed the classification of the Treatise on Invertebrate Paleontology (HERTLEIN, 1969) except where this is plainly inadequate. Classification at the familial level follows WALLER's (1978) recent thoroughgoing reappraisal of the Pteriomorphia.

The abbreviations M, OD and SD after citations of type species (and specimens) mean, respectively, type species by monotypy, type species by original designation and type species by subsequent designation.

The layout of the analysis for each species is largely self-explanatory. The attempt to determine mode of life by means of comparison with the paradigms devised in Part II is presented in Section 9 (Functional morphology) together with discussion of the function of particular shell features (partly drawing on the reasoning presented in the qualificatory section of Part II) and of other related topics.

In the synonymy lists the author has employed a modified version (presented below) of MATTHEWS' (1973) system for indicating degree of certainty and status of each reference. Although it seems complex the system is easily understood and appreciated in practice.

Where the specimens corresponding to the cited reference have been seen by the author or where the cited reference includes a description or illustration, the date of the reference is printed in normal type. The symbol v to the left of the date means that the author has seen the specimens corresponding to the cited reference. The superscript * signifies that the specimens are types of the cited species. The symbols v and v* may be preceded by the symbols ? and p (pars) implying, in the first case, that certain specimens seen by the author may correspond to those which are the subject of the cited reference, and in the second case, that the author has seen only some of the specimens corresponding to the cited reference.

Table 1: Non-ornamental parameters measured in this study (see text figs 4–6).

AH – anterior hinge length; the length of the anterior auricle measured at the hinge line (i. e. just ventral of the outer ligament).

AHL – anterior half length; the perpendicular distance between a line at right angles to the hinge line touching the shell at its most anteriorly situated point and the most ventrally situated point on the shell (not graphed for any species).

AL – separation of the auricular apices.

C – convexity (measured between the crests of plicae/costae (where present) on the right and left valves).

H – height; the maximum distance from the hinge line to the ventral margin measured in a direction perpendicular to the hinge line.

HAA – height of the anterior auricle; the total height of the anterior auricle.

HAAD – height of the anterior auricle dorsal of the hinge line.

I – intersinal distance; the distance between the deepest point in the byssal notch or sinus (the most ventrally situated point in the disc/auricle suture in *Entolium (E.) corneolum* and *E. (E.) orbiculare)* and the posterior margin measured in a direction parallel to the hinge line.

L – length; the perpendicular distance between two lines at right angles to the hinge line and tangential to the most anteriorly and posteriorly situated points on the shell.

N – depth of the byssal notch; the perpendicular distance between two lines at right angles to the hinge line and tangential to the shell at the most anteriorly situated point on the anterior auricle of the right valve and the deepest point in the byssal notch (the depth of the byssal sinus (left valve) was not measured in this study).

PH – posterior hinge length; the length of the anterior auricle measured at the hinge line (i. e. just ventral of the outer ligament).

PHL – posterior half length; the perpendicular distance between a line at right angles to the hinge line touching the shell at its most posteriorly situated point and the most ventrally situated point on the shell (not graphed for any species).

UA – umbonal angle; the angle between two lines tangential to the dorsal 'shoulders' of the disc and meeting at the apex of the umbo.

The symbols v and v* may be followed by no symbol at all or by the symbols p, non, ?, (?) and ?p. Lack of a symbol implies that the specimens corresponding to the cited reference are considered to be within the author's hypodigm for the species under discussion (as described in the relevant Section 3). The symbols p and non imply, respectively, that some and none of the specimens are considered to be within the author's hypodigm while ? implies that the specimens may be within the author's hypodigm. The symbol (?) implies less uncertainty than ?. The symbol ?p has an obvious connotation. 'No symbol', p, non, ?, (?) and ?p need not, of course, necessarily be preceded by v or v*.

Where a species is referred to only in an unillustrated faunal list and the corresponding material has not been seen by the author, the date of the reference is printed in italics. It is quite possible in some such cases to be practically certain of the affinities of the specimens (e. g. if the fauna of the horizon of derivation is well known from other sources) so such references are not preceded by a qualifying symbol, the italics being understood to convey the slight level of uncertainty. It is clear that ? and (?) are the only symbols that may precede a date in italics.

The bivariate graphs are intended to illustrate the variation and, as far as this can be done with 'static' plots (Cock, 1966), the ontogeny of the various shell dimensions. A minimum requirement of 7–10 points was set for the inclusion of such graphs. Where they differ between the valves, right and left values vor any given parameter are separated and denoted by addition of the letter R or L as a subscript to the abbreviated name of the parameter. (Although there is no difference between the valves, right and left valve values for the intersinal distance in *Entolium (E.) corneolum* are plotted separately for the purposes of comparison with *E. (E.) lunare*.) Numbers in the graphs refer to points immediately above and to the left of them and correspond to numbers in the text accompanying citations of certain important (usually type) specimens or figures of specimens. The graduations on the axes are in millimetres in all cases except for UA, where the graduations are in degrees. Apart from in the case of the parameter UA, length has been employed as the standard measure of size except where this generates too few points for inclusion, in which case height has been employed. It was felt at the time of draughting that umbonal angle was not entirely independent of length so this parameter was plotted against height rather than length wherever sufficient data presented itself. Subsequent consideration suggests, in fact, that umbonal angle and length are independent of each other in all real situations.

Where plical frequency histograms have been plotted, plical counts for right and left valves have been plotted together where the minimum plical count is 12 or more, even though there may be a difference of one plica between the valves. Where there is a difference between the valves and the minimum number of plicae is less than 12, values for right and left valves have been separated and only one set plotted (the letter R or L is added as a subscript to PL as appropriate).

The single histogram for IC *(Propeamussium (P.) pumilum)* uses both right and left valve data so no subscript is added to the abbreviation. However, the single graph involving EC *(P. (P.) laeviradiatum)* uses only left valve data so the letter L is added as a subscript to EC.

The locations and museum registration numbers of specimens represented in the bivariate plots and histograms can be obtained from the author on request.

Table 2: Explanation of abbreviated museum (and individual collection) names and lists of works whose partial or complete subject is pectinids and/or propeamussiids preserved in the museums.

BCM : City of Bristol Museum and Art Gallery (J. Sowerby, 1812–22).

BM : British Museum (Natural History), London (Arkell, 1929a–35a; Cox, 1935a, 1936a, 1952; Damon, 1880; Duff, 1978; Lycett, 1863; Neale, 1956; Paris and Richardson, 1916; J. Sowerby, 1812–22; J. de C. Sowerby, 1822a–46a, 1840b; Whidborne, 1883; Witchell, 1880).

BSPHG : Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich (Boehm, 1883; Burckhardt, 1903; Goldfuss, 1833–40; Kühn, 1935, 1936; Rothpletz, 1886; Schlippe, 1888; Waagen, 1867; Yamani, 1975).

DM : Institut des Sciences de la Terre, Université de Dijon.

ENSM : École Nationale Supérieure des Mines, Centre d'Études et de Recherches de Paléontologie Biostratigraphique, Université de Paris-Sud, Centre d'Orsay (Buvignier, 1852; Bayle, 1878; Dolleus, 1863; Douvillé, 1916; Terquem and Jourdy, 1869).

GPIB : Institut für Paläontologie der Rhein. Friedr.-Wilhelms Universität, Bonn (Goldfuss, 1833–40).

GPIG : Geologisch-Paläontologisches Institut und Museum der Georg-August-Universität, Göttingen (Ernst, 1923).

GPIT : Universität Tübingen, Institut und Museum für Geologie und Paläontologie (Oppel, 1853; Quenstedt, 1858; Rollier, 1915; Staesche, 1926).

HM : Museum für Naturkunde an der Humboldt-Universität zu Berlin (Schlotheim, 1820).

IGS : Institute of Geological Sciences, Geological Survey, London (Hull, 1857; Melville, 1956; Morris and Lycett, 1851–55; Tawney, 1866).

MHNL : Museum d'Histoire Naturelle, Lyon (Dumortier, 1864–74).

MN : Museum Nationale d'Histoire Naturelle, Paris (Lamarck, 1819).

MNO : Museum Nationale d'Histoire Naturelle, Paris, d'Orbigny Collection (d'Orbigny, 1850).

MNP : Museum Nationale d'Histoire Naturelle, Paris, Peron Collection (Peron, 1905).

MNR : Museum Nationale d'Histoire Naturelle, Paris, Regional Collection.

MNS : Museum Nationale d'Histoire Naturelle, Paris, Systematic Collection (Cotteau, 1853; J.-C. Fischer, 1964; de Loriol, 1894, 1904; de Loriol and Lambert, 1893; de Loriol et al., 1872).

NM : École nationale Supérieure de Geologie, Nancy (Buvignier, 1852; Dechaseaux, 1936).

NMW : Naturhistorisches Museum, Vienna (Neumayr, 1871).

OUM : Oxford University Museum (Arkell, 1926, 1929a–35a; Douglas and Arkell, 1932; Duff, 1978; Kirkaldy, 1963).

SbM : Woodend Museum, Scarborough.

ScM : Scunthorpe Museum and Art Gallery.

SM : Sedgwick Museum, Cambridge (Whidborne, 1883).

WM : Whitby Museum (Simpson, 1884).

YM : Yorkshire Museum, York (Phillips, 1829).

Cretaceous	c		
Tithonian *	▽		▤
Kimmeridgian *	◆		
Oxfordian	●	◐	
Callovian	○		⊞
Bathonian	□		
Bajocian	▲	◭	
Aalenian	△		
Toarcian	■		⬓
U Pliensbachian	⬘		
L Pliensbachian	◇	◧	
Sinemurian	×		
Hettangian	▼		
Rhaetic (Triassic)	r		

Table 3: Key to symbols used in graphs and diagrams (*the sense in wic these stage names are applied is explained on p. 16).

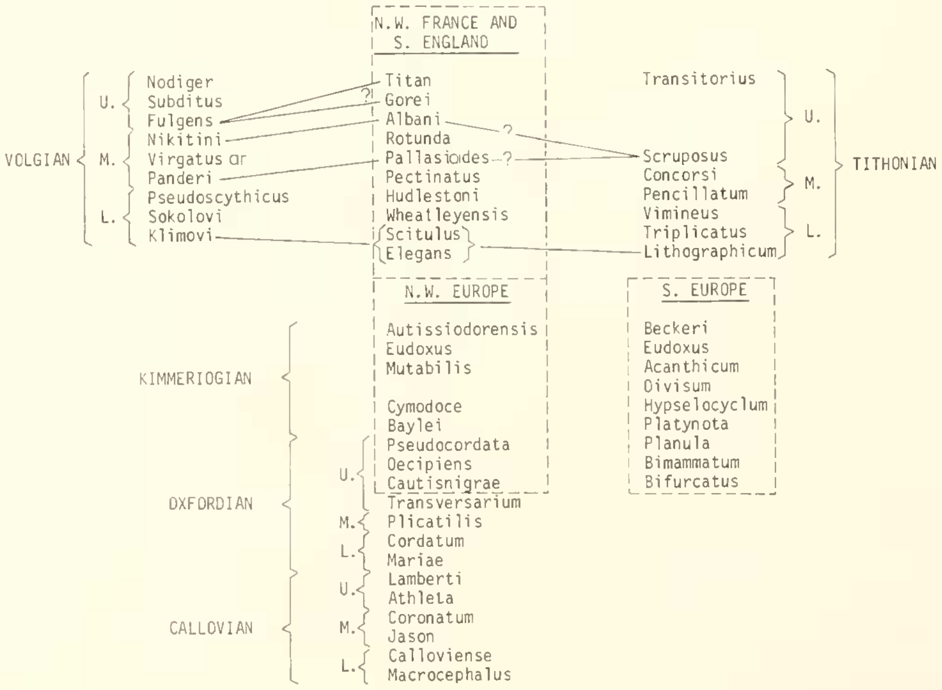
The abbrevations of museum names (and of the names of particular collections in museums) used herein are listed and explained in Table 2 together with works whose partial or complete subject is Jurassic scallops preserved in the various museums. Non-parenthesised numbers following museum abbreviations in the text refer to individual specimens or small 'collectives' in a single tray except in the case of YM where the number refers to a box. Unfortunately in a number of museums unfigured material is not catalogued thus where reference is made to such material no more than the identity of the museum can be indicated. Where more than one specimen is involved as a reference to museum material and the actual number is of some importance, it is quoted in square brackets.

The species distribution maps have been compiled very largely from the citations listed in the synonymies. Details concerning the remaining information (derived from collections) can be obtained from the author on request. The reconstructions employed as the basis for charting extra-European distribution are those of Smith and Briden (1977). In the absence of precise details concerning place of discovery, specimens from the Caucasus (Pompeckj, 1897) have been symbolised on both the north and south sides of Tethys.

The symbols used in both the graphs and the maps to indicate stratigraphic horizon are explained in Table 3. Although the general lack of stratigraphic subdivision beyond the level of the stage masks some of the temporal changes in morphology and distribution mentioned in the text, it was felt that the plethora of symbols required to illustrate such changes would prevent appreciation of the larger scale changes.

The L. and U. Pliensbachian have traditionally been regarded as subdivisions of almost stage rank. Separate symbols are therefore used for specimens from the L. and U. Pliensbachian in exception to the general rule of using the same symbol for specimens from all substages of a stage.

The zonal stratigraphic scheme presented in Table 4 and used throughout is that of Hallam (1975a). The author has followed Hallam in not recognising the Portlandian stage. Sediments in S. England and N. W. France which would traditionally be termed Portlandian are herein termed Tithonian. The term Kimmeridgian is applied sensu gallico (= L. Kimmeridgian sensu anglico).



BATHONIAN	U.	Discus
		Aspidoides
		Retrocostatum
	M.	Morrisi
		Subcontractus
	L.	Progracilis
		Zigzag
BAJOCIAN	U.	Parkinsoni
		Garantiana
		Subfurcatum
	L.	Humphriesianum
		Sauzei
		Laeviuscula
		Discites
AALENIAN		Concavum
		Murchisonae
		Opalinum
TOARCIAN	U.	Levesquei
		Thouarense
		Variabilis
	L.	Bifrons
		Falciferum
		Tenuicostatum
PLIENSBACHIAN	U.	Spinatum
		Margaritatus
	L.	Davoei
		Ibex
		Jamesoni
SINEMURIAN	U.	Raricostatum
		Oxynotum
		Obtusum
	L.	Turneri
		Semicostatum
		Bucklandi
HETTANGIAN		Angulata
		Liasicus
		Planorbis

Table 4: Zonal scheme (after Hallam, 1975 a) for the European Jurassic (see p. 16).

Appendix I is a list of those nominal pectinid and propeamussiid species described from the Jurassic of Europe which are not considered herein. Apart from names created for members of the highly distinctive group of species from the Tithonian of alpine and southern Europe and for members of the genus *Weyla* (see p. 11) it consists of names created for specimens which in the author's opinion are specifically indeterminate and names which, as a result of poor descriptions and figures and the unknown whereabouts of type material, can only be said to refer to 'pectinids' or 'propeamussiids'.

NOTE ON COPPER ENGRAVINGS

Many of the illustrations in the earlier works referred to herein were printed from copper engravings. Since this process involves reversal of the image it follows that for accurate reproduction the engraving must be a mirror image of the original specimen. A number of peculiar illustrations encountered in the course of research were quite clearly the result of a failure to make the initial reversal. In such cases measurements have been automatically reversed and in general no further comment has been made in the text.

I am grateful to R. J. Cleevely (British Museum; Nat. Hist.) for pointing out to me the reason for reversed illustrations.

II. MORPHOLOGICAL PARADIGMS FOR THE BASIC MODES OF LIFE OF SCALLOPS

The background to the inclusion of this piece is presented on p. 11 together with an explanation of the sense in which the term 'paradigm' is applied herein. The mode of life categories are a combination of those of Kaufmann (1969) and Stanley (1970). Although some living pectinids are known to be cemented (e. g. *Hinnites*) no paradigm is presented for this mode of life because it is easily recognisable in fossils from preservation. In formulating the paradigms the author has restricted his attention to easily observable external features of the shell.

Size of the antero- and posterodorsal disc gapes has therefore not been considered. This might be thought to represent an important omission in connection with the swimming paradigm. In fact it is probably of little consequence, for, as Waller (1969) has pointed out, the jets of water expelled during swimming are actually controlled by the apposed velar lobes of the antero- und posterodorsal parts of the shell. It should be pointed out that swimming is quite possible in forms completely lacking disc gapes (e. g. *Gloripallium pallium* [see Waller, 1972 b]).

Many living scallops actually have more than one mode of life (e. g. byssal swinging/tightly byssate, reclining/swimming) so this possibility has to be borne in mind in comparing fossil species to the paradigms. It is doubtful whether swimming could ever be a full-time activity and certainly no living scallops have yet been discovered in which swimming is the exclusive mode of life.

RECLINING

Reclining is defined as lying on the sea floor without any means of attachment. All known living species with this habit lie on the right valve. In the lack of a means of attachment reclining species are susceptible to overturning and transport in high energy environments. This danger can be offset by having a large thick shell (increasing weight) with strong ornamentation on the right valve (increasing frictional resistance to movement). Low ornamentation on the left valve and generally low convexity will also help to lessen the risk of overturning and transport by reducing the profile of the shell and consequently its resistance to water movements. Given an inability to orientate the shell with respect to the direction of water movements an orbicular shape will be the best form for the disc as far as minimising the risk of overturning is concerned. A low convexity, orbicular disc is also the best form for reclining in low energy environments where the substrate is soft, since it spreads the weight of the shell and thereby inhibits sinkage. Small size (large surface area/weight ratio) and a thin shell will be similarly beneficial in this situation and strong ornament will be a disadvantage unless it extends beyond the disc margins as some form of protuberance with a high surface area/weight ratio and thus provides a 'snowshoe' effect. Large auricles would provide the same benefit on soft substrates but otherwise no advantage can be envisaged in their possession for a standard reclining mode of life.

TIGHT BYSSAL FIXATION

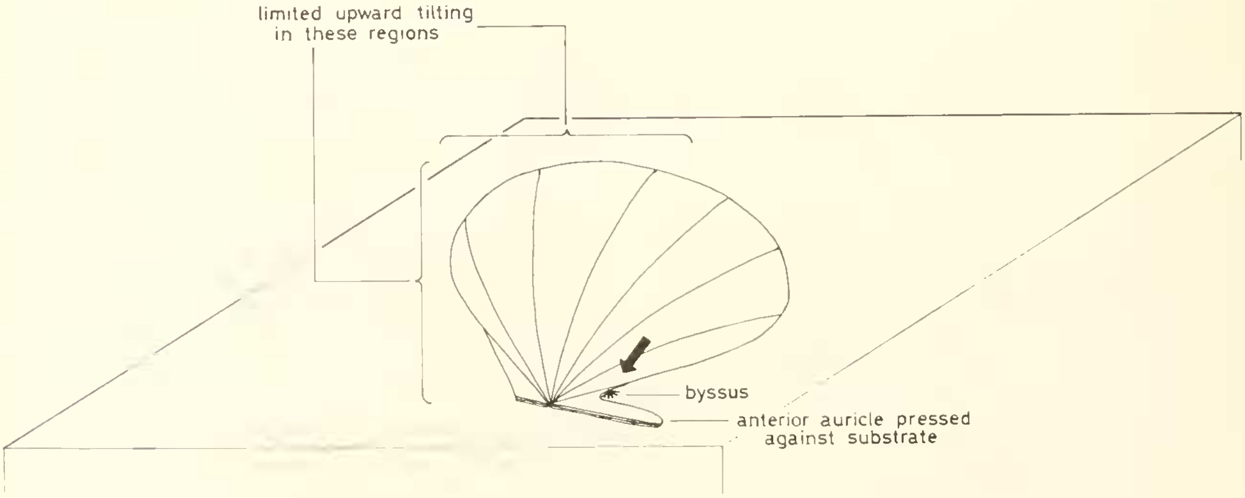
Tightly byssate scallops apply the right valve to the substrate and extend a short byssus over the margin of the right valve at the base of the anterior auricle. The great majority of living species attach themselves beneath or on the sides of hard objects.

Unless the right valve is of very low convexity any increase in the tension of the byssal (= pedal) retractor muscle beyond that strictly required to keep the animal in contact with the substrate tends to tilt the shell and present a large area for resistance to currents. There is thus a danger that the attachment will be broken altogether. Tilting in a purely anterior-posterior sense can be minimised by having a small anterior auricle thus bringing the byssus closer to the tilting fulcrum and minimising its leverage. This, however, does nothing to minimise upward tilting of the ventral part of the shell and a better all-round solution (text fig. 7) is elongation of the dorsal part of the anterior auricle without addition to the ventral part (i. e. development of a deep byssal notch). A further improvement is achieved by a 'rightward' slope of the anterior auricle from posterior to anterior (WALLER, 1972b). Possession of a narrow disc restricts the shell area presented to currents upon tilting.

Development of a deep byssal notch has the added advantage of putting the byssus in a position where it can resist an overturning force (such as that provided by currents meeting a convex right valve) acting on the posterior part of the shell (STANLEY, 1970). However, assuming that it is impossible to increase the force exerted through the byssus it will be necessary in this situation for the depth of the byssal notch to increase allometrically (exponent 2) in order to maintain an attachment at all, since the moment exerted by the overturning force will be proportional to the cross-sectional area of shell perpendicular to its line of action.

Obviously possession of an initially deep byssal notch will create a certain amount of leeway, in forms lacking allometric growth of the byssal notch, before attachment is actually lost. With regard to the assumption concerning the force exerted through the byssus (i. e. that it is impossible to add to the number of byssal fibres so as to increase the basic strength of the byssus, and that of the bond between byssus and substrate, and thereby allow a greater force to be exerted by the byssal retractor without breaking the attachment) it must be doubted whether this is universally applicable. The assumption is made in the interests of facilitating at least some sort of interpretation of fossil morphologies. Although the limited information on living scallops suggests that the assumption is reasonable, it is difficult to see why scallops should be constrained to retain the juvenile number of byssal threads.

The author is here only considering forms with the usual attachment position, beneath or against the sides of objects. The effective overturning moment will actually decrease during ontogeny in forms attached to the upper surfaces of objects since in this situation the overturning force has to contend



Text fig. 7: The effect of elongation of the dorsal part of the anterior auricle in restricting tilting (resulting from the combination of high byssal tension and a convex right valve) in the posterior and posteroventral shell regions (arrow = byssal force).

with the weight of the animal (scaling as L^3). For all orientations on hard, smooth substrates it will be advantageous to have a minimally ornamented right valve so as to maximise the shell area in contact with the substrate and consequently maximise frictional resistance to lateral movement of the shell. On soft substrates frictional resistance will be increased by the development of some form of ornament that penetrates the substrate surface. Similar ornament on the left valve will also be of value if the substrate is so soft the the animal can insinuate itself. Otherwise it will be preferable for the ornament of the left valve to be subdued so as to minimise resistance to currents and consequently maintain lateral strain on the byssus at a tolerable level. A low convexity left valve will be advantageous for the same reason. In forms with the usual attachment position (see above) small size and thin valves will be beneficial in minimising the basic strain on the byssus resulting from the weight of the animal.

For forms tightly attached in confined spaces where the left valve comes into contact with the substrate upon gaping it will be advantageous for the hinge line to migrate ventrally so as to prevent restriction of the angle of gape with growth (Yonge, 1951).

Implied here are fissures that are essentially 'v'-shaped. Narrow, parallel-sided spaces are not colonisable, except by small forms, because shell growth rapidly makes it impossible to open the valves.

At all sizes subdued ornamentation and low convexity of the left valve together with a thin shell will allow the widest possible gape in the space available. Subdued ornament and low convexity will also maximise frictional resistance to movement if the substrate is hard and smooth (see above).

BYSSAL SWINGING

The nature of a byssal swinging mode of life needs no explanation. As in tightly fixed forms (see above) the byssus is extended between the valves at the base of the anterior auricle. In the absence of contact between the shell and the substrate to which the byssus is attached there is nothing to be gained from elongation of the dorsal part of the right valve anterior auricle and consequent production of a deep byssal notch. Strain on the byssus as the result of frictional drag between the shell and currents can be minimised by development of a low convexity posteriorly elongated disc (i. e. a shape that behaves like a windvane [Kaufmann, 1969]) on which the ornament is subdued. Small size and thin valves will minimise the basic strain on the byssus resulting from the weight of the shell.

SWIMMING

Scallops achieve self-propulsion through the water in two ways. In one the valves clap together rapidly and a large volume of water is expelled ventrally; the shell therefore moves dorsally. Rapid adduction is also involved in the other method but here the velae (the muscular curtains formed from the inner mantle lobe of each valve) are employed in such a way as to restrict egress of the water to two small regions on either side of the auricles (see p. 17). Movement is therefore in a ventralward direction. In both processes the left valve is always uppermost. The first process, the 'escape response' of authors, is rarely observed in nature and will not be considered further. The second process is that which has come to be known as 'swimming'.

In the swimming process thrust can be maximised by possession of low convexity valves so that almost all the water trapped between the valves is finally expelled (Thayer, 1972). Low convexity also minimises drag in the brief, post-adductive planing phase by rendering the shell streamlined. Since scallops are denser than water they must generate lift in order to progress by swimming. At the expense of forward advance this can be achieved simply by tilting the dorsal part of the shell downwards and thus translating some of the thrust from the water jets into an uplifting force. By departing from a paradigmatic form for generating thrust and minimising drag, lift may also be obtained hydrodynamically in the planing phase. A strongly right convex shell thrust through the water would generate lift in the same way as an angled board but such a shape would have such a poor thrust/drag ratio that, in spite of allowing jetting of water at a lower angle, it is very doubtful whether it could travel as far horizontally for a given expenditure of energy as a low convexity shell gaining lift purely from downward thrust. A shell of low right valve convexity but with moderate left valve convexity (a 'hydrofoil' shape) would also generate lift (by the Bernoulli Effect Stanley, 1970]) and in this case it seems likely that the thrust/drag ratio would not be so poor as to greatly counteract the advantage of a lower 'required jetting angle' and that therefore such a shell would travel at least as far horizontally for a given expenditure of energy as a shell with both valves of low convexity, gaining lift purely from downward thrust.

Since gravity scales as L^3 while thrust and lift (together with drag) only scale as L^2 it becomes steadily more difficult for scallops to swim as they approach large size (Gould, 1971). The size at which the capacity is lost can be increased by various muscular allometries (Gould, 1971; Thayer, 1972). As far as the hard parts are concerned swimming ability can be prolonged by ontogenetic increase in the umbonal angle, which serves to direct the water jets more nearly backwards and therefore maximises forward thrust (Stanley, 1970), and by length/height allometry, which increases the 'aspect ratio' and thereby minimises drag (Gould, 1971). Obviously an initially large umbonal angle and length/height ratio (i. e. in general terms a sub-orbicular rather than sub-ovate shape) will make for more efficient swimming in the juvenile and add to the effects of allometry in the adult. Further advantages are a thin shell (reducing weight) and subdued ornament (reducing drag). Large auricles would increase the resistance of the shell to sinking during the planing phase but would increase drag without adding anything to thrust or lift so it is very doubtful whether they would provide an overall advantage.

QUALIFICATORY SECTION CONCERNING ORNAMENT

It will have been noted in the foregoing sections that strong ornament is an advantage for stability in certain situations. A number of other ways have been suggested in which strong ornamentation, in the form of radial plicae, might be beneficial to a scallop and it is as well to evaluate whether such ornament could indeed be of use in any other way for if so it will be necessary to play down the evidence of ornament, where developed as radial plicae, in attempting to determine mode of life by means of the paradigms.

The most popular suggestions have been that plicae reduce the risk of the shell being broken (on the assumption that they increase strength in the same way as corrugations in a sheet of iron) by forces acting on it during life. On the grounds of results obtained by Preuschoft et al. (1975) from stress experiments, Reif (1978) has recently asserted that the basic assumption that plicae increase the overall strength of a shell is false and he has gone so far as to say that plicae actually decrease the overall strength of a shell. Such are in fact by no means necessary conclusions from the experimental results of Preuschoft et al. The experiments performed by the latter authors consisted of the application of a force above the adductor muscle (to simulate the force exerted by the adductor during swimming) of previously 'stress-coated' scallops. (A stress-coat is a lacquer which cracks to show up lines of tension and compression on a stressed body.) The observed stress pattern indicated that plicae do indeed increase strength in the ventral sector but that they reduce strength in the dorsal sector. It can therefore be said that plicae do not increase the strength of a shell throughout and, since plicae actually weaken the shell in the dorsal sector, it can be said, on the assumption that the thickness and therefore basic strength of the shell in the dorsal sector is the same as in the ventral sector (and bearing in mind the fact that a shell is only as strong as its weakest point), that the overall strength of the shell is reduced by the development of plicae. The foregoing assumption, which Reif must have made to reach such conclusions as he did from the experimental results of Preuschoft et al., is in fact invalid for at least a large number of species *(Pecten maximus,* one of the species used by Preuschoft et al., being a particularly good example of a species with markedly greater shell thickness in the dorsal sector) and taking into account the fact that the number of shell layers increases from the ventral to the dorsal margin (Taylor et al., 1969) it seems practically certain to be generally invalid. If it is invalid to make the above-mentioned assumption then one is in no way forced by the results of the stress-coat experiments to draw the conclusion that plicae reduce the overall strength of a shell, for such experiments do not provide quantitative data to tell us whether plicae reduce strength in the dorsal sector to a value below that of unplicated shell in the ventral sector, which is the crucial point in deciding whether plicae increase or decrease the overall strength of a shell.

The whole question of whether plicae do or do not increase the overall strength of a shell is potentially answerable through breakage experiments with plicate and non-plicate shells of equal thickness and convexity (structural strength is enhanced by increased convexity [J. Currey, pers. comm. 1978]). The author has yet to find appropriate material for properly controlled experiments but crude hand trials using plicate and non-plicate shells of roughly equal thickness and convexity (belonging respectively to the extant species *Chlamys opercularis* and *Ch. tigerina)* indicate strongly that plicae do increase overall strength (at least for those species [probably the very great majority; see above] whose shells are dorsally thickened to the same moderate extent as in *Ch. opercularis).*

Although it now seems likely that the traditional assumption that plicae increase the overall strength of a shell is by and large valid, this does not necessarily imply that the risk of breakage by forces acting on the shell during life is ever reduced by the development of plicae. A non-plicate shell may be quite adequate to withstand the forces. This certainly seems to be the case for the force generated in swimming (see above) for there exist actively swimming non-plicate pectinids of quite average shell thickness and convexity (e. g. *Placopecten magellanicus* [see Stanley, 1970]) in which there is no evidence of shell breakage during swimming. It also seems likely that all but the thinnest-shelled of scallops could withstand wave-generated forces up to the greatest magnitudes typically encountered, without the additional strength provided by plicae (cf. Verrill, 1897). Stanley (1970) has shown that a non-plicate shell of comparable thickness to that of an average scallop, if of somewhat greater convexity (that of *Mytilus edulis),* is strong enough to withstand wave forces of a magnitude far greater than any likely to be experienced by the majority of scallops (those developed on an exposed inter-tidial zone – most scallops are unable to colonise the inter-tidal zone because their permanent gapes do not allow retention of water [to prevent tissue dehydration] between high tides). It is however probable that a non-plicate scallop shell of average thickness and convexity would be in great danger of being broken by predator-generated forces (as suggested originally by Verrill, 1897). Extra-orally feeding starfish, which are certainly a major enemy of scallops in temperate waters at the present time (Medcof and Bourne, 1964; Feder, 1970; Bloom, 1975), are known to be capable of generating forces up to 5.5 kg (Feder and Christensen, 1966) in their efforts to pull bivalves apart (in order to facilitate entry of the stomach) and Carter (1968) reports shell breakage in the genus *Venerupis* (thicker and more inflated than typical scallops) as the result of attempted starfish predation. G. J. Vermeij (pers. comm., 1978) reports that extra-orally feeding starfish are rare in the tropics and therefore may not constitute a serious threat in these regions. He adds however that durophagous teleosts are a major enemy of scallops in the tropics and such fish, which are capable of biting off chunks of coral (Stanley, 1970) would surely be able to crush non-plicate scallops of average thickness and convexity. Of the other animals which are known to be enemies of scallops at the present time (intra-orally feeding starfish [Brun, 1972]; plaice and cod [Medcof and Bourne, 1964]; herring gulls [Gutsell, 1931]; sea anemones, octopods and crabs [Bloom, 1975]) it seems very likely that octopods and crabs would also be able to crush non-plicate scallops of thickness and convexity equivalent to plicate forms.

Although it seems likely that plicae would be of benefit to a scallop of average thickness and convexity as far as passive resistance to attempted predation is concerned they would be disadvantageous (increasing drag) as far as the actual evasion of predators by swimming is concerned. (The use of the swimming response as a means of escape from predators is a well documented phenomenon [e. g. Thomas and Gruffydd, 1976].) It is possible to imagine that a smooth shell might in fact be just as good an adaptation towards predators as a strongly plicate shell because of its greater suitability for swimming. The abandonment of plication and the development of internal costae (which must surely strengthen the shell, albeit at somewhat greater material cost than plicae) in certain genera of scallops (e. g. *Amusium)* would seem to represent an attempt to gain the best of both worlds.

Propeamussium also possesses internal costae and lacks plicae. However in this case plicae may be absent for constructional rather than functional reasons. Waller (1972a) is of the opinion that plicae could not be developed in a shell, such as that of *Propeamussium*, with an outer prismatic layer in one or both valves.

The development of layers of divaricate fibres (which in conjunction with the usual layers of radially arranged foliae must produce a relatively strong structure by analogy with plywood) in the shells of certain non-plicate *Entolium* and *Camptonectes* species might also represent an attempt to facilitate a 'siege' policy towards predators without at the same time impairing a 'fugitive' policy.

It has been suggested that plicae might be beneficial for resisting attempted predation in ways other than by increasing shell strength. Reif (1978) has suggested that by interlocking at the commissure plicae might prevent lateral twisting of the valves by starfish. Quite apart from the fact that there is no evidence that starfish ever attempt to twist the valves apart to gain access to the soft parts (the only technique recorded being a simple pull against the action of the adductor [Feder and Christensen, 1966]) it must be doubted whether the long outer ligament of scallops would not perform this task quite adequately and thus obviate any need for further adaptation of the shell.

It should be noted that the scallop adductor is able to resist an opening force applied by a starfish for long periods (author's observations) so provided that the period of time which a starfish will devote to an attempt to open a scallop is sometimes less than the length of time for which the adductor can offer resistance (a not unreasonable assumption [cf. Burnett, 1960]) increased shell strength will undoubtedly be beneficial in the context of this form of predation (as suggested on p. 20).

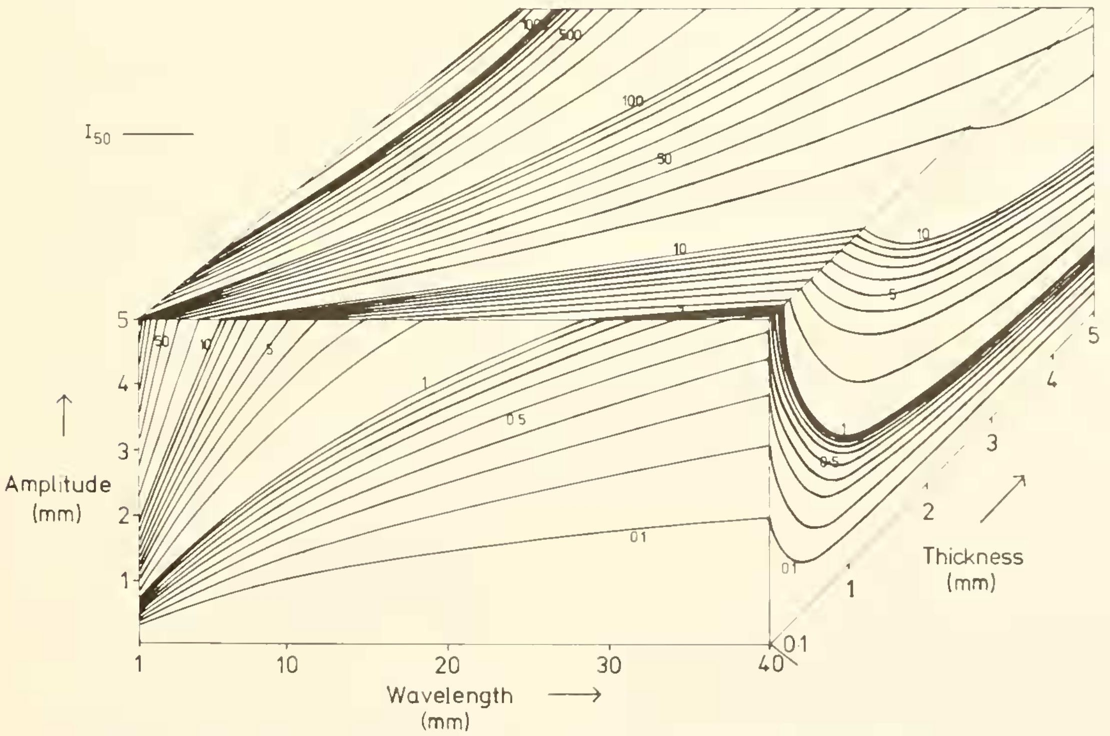
Carter (1968) has suggested that in the case of a failure to open the valves widely an undulating shell margin (as is associated with plication) might serve to prevent introduction of more than a small part of a starfish's stomach into a bivalve. As Stanley (1970) has pointed out, the stomach of a starfish is so flexible that it is in fact very unlikely that its introduction would be severely hampered by an undulating shell margin.

One further way in which it has been suggested that plicae might be beneficial to a scallop is through their enlarging effect on the area of mantle tissue and thus of respiratory surface (Waller, 1969). It remains to be demonstrated whether a larger respiratory surface is of any particular benefit to a scallop.

To sum up the foregoing, in most of the ways suggested it is unlikely that plicae would be an advantage for a scallop. However, in the case of passive resistance to attempted predation it is quite likely that they would be of benefit to forms of average thickness and convexity, so in accordance with the approach advocated on p. 19 the author has tended to disregard the evidence of strong ornament in the form of radial plicae in attempting to determine mode of life by means of comparison with the paradigms.

Extra-orally feeding starfish, at least, have been in existence as long as scallops (they are known from the U. Ordovician [Vermeij, 1977]) so the possession of plicae would seem always to have been beneficial to forms of average thickness and convexity in a context other than that of stability.

Corrugations increase the strength of a sheet of material by increasing its moment of inertia (Wainwright et al., 1976). It can be seen from text fig. 8 (which shows moment of inertia values [I_{50}] for a range of sinusoidally corrugated sections of arbitrary length 50 mm; the means by which I_{50} values were derived is presented in Appendix II) that for a sheet of any given thickness, corrugations of high amplitude and low wavelength give the greater increase in strength and it can therefore be inferred that plicae of high amplitude and low wavelength will be paradigmatic for passive resistance to at-



Text fig. 8: Moment of inertia (I_{50}) for a range of sinusoidally corrugated sections of length 50 mm (see Appendix II). Surfaces of equal I_{50} would all slope generally towards the left and back if drawn in.

tempted predation. It can also be seen from text fig. 8 that plical intercalation will increase strength (through shortening wavelength) and will thus be of value as the animal grows and the potential leverage which a predator can exert to break the shell increases.

It should be noted that it is only the strength in bending which is greater than that of a flat plate of equivalent thickness and then only when bending is about the x–x axis of the corrugated section. This is in fact the most likely situation in any form of predatory attack on a plicate shell. It should be further noted that corrugations also increase stiffness. This property may in fact be just as important as strength in the context of resisting attempted predation by animals, such as extra-orally feeding starfish, which attempt to pull the valves apart rather than crush them.

It seems very likely that forms of continuous comarginal ornament involving thickening of the shell (e. g. comarginal lamellae) would result in an increase in overall strength and thus be of benefit to a scallop of average thickness and convexity in the context of passive resistance to attempted predation. The evidence of such ornament as continuous comarginal lamellae has therefore been played down, in the same way as for radial plicae, in attempting to determine mode of life by means of comparison with the paradigms.

In conjunction with some form of radial or divaricate ornament and against a background of appropriate 'grain' size, discontinuous comarginal lamellae (and to a rather lesser extent continuous comarginal lamellae) tend to camouflage a shell somewhat to the human eye. It cannot yet be said whether discontinuous comarginal lamellae actually camouflage the shell to visual predators (and thus whether the development of such ornament would be beneficial to a scallop in the context of avoiding predation) so in attempting to determine mode of life by means of comparison with the paradigms the author has not disregarded the evidence of discontinuous comarginal ornament except where it is at odds with the evidence of other aspects of morphology or with ecology.

III. SYSTEMATIC PALAEOBIOLOGY OF THE 'EUROPEAN JURASSIC' PECTINIDAE AND PROPEAMUSSIIDAE

FAMILIAL DIAGNOSES

Waller (1978) provides the following familial diagnoses:

Propeamussiidae – 'Byssate or free Pectinacea with outer, simple-prismatic calcitic layer on right valve present on main portion of disk throughout ontogeny; crossed-lamellar aragonite extending outside of pallial line, in some cases nearly to distal margins, and commonly covering hinge plate. Byssal notch without ctenolium even in early growth stages (now known to be present in one species – T. R. Waller, pers. comm. 1980). Mantle curtains commonly without guard tentacles'.

Pectinidae – 'Byssate, cemented, or unattached Pectinacea with outer, simple-prismatic calcitic layer on right valve generally present only in early growth stages, rarely absent altogether; crossed-lamellar aragonite restricted to area inside of pallial line or absent. Byssal notch with ctenolium, at least at early growth stage. Mantle curtains bearing guard tentacles'.

Family PROPEAMUSSIIDAE Tucker Abbott 1954
Genus *PROPEAMUSSIUM* De Gregorio 1884

Type species. OD; De Gregorio 1884, p. 1; *Pecten (Propeamussium) Ceciliae* De Gregorio 1884, p. 1; Miocene, Sicily.

AMENDED DIAGNOSIS

'Small, thin, valves nearly equally convex; sculptured with concentric lines, LV commonly with radial striae or riblets; byssal notch moderately deep to slight; right anterior auricle of some shells with radial riblets; interior with radial riblets which usually extend to middle or to margin. L. Jur. – Rec., cosmop.' (Hertlein, 1969: N350).

Subgenus *PROPEAMUSSIUM* s. s.

(Synonyms etc. *Propeamusium* Dall 1886 [nom. van.]
Propreamusium Jackson 1890 [nom. null.]
Paramusium Verrill 1897
Paramussium De Gregorio 1898 [nom. null.]
Propeannessium Cossmann and Pisarro 1906 [nom. null.]
Occultamussium Korobkov 1937
Pseudopalliorum Oyama 1944
Flavamussium Oyama 1951
Actinopecten Bonarelli 1951)

AMENDED DIAGNOSIS

'Valves rather flattened, usually gaping along lateral margins; byssal notch slight; internal ribs extend about half way (farther in some) to margin. L. Jur. – Rec., cosmop.' (Hertlein 1969: N350)

DISCUSSION

In the Jurassic *P. (Propeamussium)* can be divided into three groups on the following basis:

1. 9–13 original internal costae terminating at approximately 7/8 H; dorsal margins of right valve extended slightly beyond hinge-line.
(= *P. (P.) pumilum)*.
2. 9–10 original internal costae terminating at approximately 7/8 H; dorsal margins of right valve extended into horn-like processes.
(= *P. (P.) laeviradiatum)*.
3. 7–9 original internal costae increasing in number by intercalation to 18, terminating at approximately 5/6 H; ap-

proximately straight dorsal margin in right valve. (= *P. (P.) nonarium*).

Propeamussium (Propeamussium) pumilum (Lamarck 1819)

Pl. 1, Figs. 1–4, 7–9; text figs. 9–12.

Synonymy

1819 *Pecten pumilus* sp. nov; Lamarck, p. 183.
(?) 1825a *Pecten incrustatus* sp. nov; Defrance, p. 253.
(?) 1828 *Pecten intusradiatus* sp. nov; Münster in Keferstein, p. 574.
(?) 1832 *Pecten intusstriatus* sp. nov; Münster in De La Beche, p. 386.
1832 *Pecten contrarius* sp. nov; v. Buch in De La Beche, p. 412, 423.
1833 *Pecten personatus* sp. nov; Goldfuss in Zieten, p. 68, pl. 52, figs. 2a, 2b.
v* 1836 *Pecten paradoxus* sp. nov; Münster in Goldfuss, p. 74, pl. 99, figs. 4a–f.
1836 *Pecten personatus* Goldfuss; Goldfuss, p. 75, pl. 99, fig. 5.
1839 *Pecten personatus* Goldfuss; v. Buch, p. 101.
v 1850 *Pecten pumilus* Lamarck; d'Orbigny, p. 257.
1852 *Pecten incrustans* Defrance; Bronn, p. 213, pl. 19, figs. 5a–c.
v 1852 *Pecten personatus* Goldfuss; Quenstedt, p. 505, pl. 40, fig. 39.
non 1853 *Pecten personatus* Goldfuss; Morris and Lycett, p. 11, pl. 1, figs. 17, 17a.
v* 1853 *Pecten amalthei* sp. nov; Oppel, p. 77, pl. 4, fig. 9.
1858 *Pecten incrustatus* Defrance; Oppel, p. 262.
1858 *Pecten pumilus* Lamarck; Oppel, p. 419.
v 1858 *Pecten contrarius* v. Buch, Quenstedt, p. 258, pl. 36, figs. 15–17.
1858 *Pecten undenarius* sp. nov; Quenstedt, p. 321, pl. 44, fig. 14.
v 1858 *Pecten personatus* Goldfuss; Quenstedt, p. 337, pl. 46, figs. 21–24.
1860 *Pecten pumilus* Lamarck; Coquand, p. 64.
? 1861 *Pecten amaltheus* Oppel; Stoliczka, p. 198, pl. 6, fig. 7.
1864 *Pecten pumilus* Lamarck; v. Seebach, p. 96.
1867 *Pecten pumilus* Lamarck; Waagen, p. 630.
(?) 1868 *Pecten Dumortieri* sp. nov; Jaubert, p. 234.
? 1871 *Pecten penninicus* sp. nov; Neumayr, p. 375, pl. 24, fig. 4.
1871 *Pecten pumilus* Lamarck; Brauns, p. 396.
1874 *Pecten pumilus* Lamarck; Dumortier, p. 195, pl. 44, figs. 1–5.
1874 *Pecten Agathis* sp. nov; Gemmellaro, p. 107, pl. 13, figs. 3, 4.
1876 *Pecten pumilus* Lamarck; Tate and Blake, p. 364.
1886 *Pecten (Amussium) incrustatus* Defrance; Gemmellaro, pp. 163, 352.
1886a *Pecten pumilus* var. *ergolus* var. nov; De Gregorio, p. 670, pl. 1, fig. 10.
1891 *Pecten (Amussium) paradoxus* Münster; Behrendsen, p. 393.
1894 *Amusium paradoxum* (Münster), Möricke, p. 38.
1897 *Pecten personatus* Goldfuss; Pompeckj, p. 779.
1897 *Pecten* cf. *contrarius* v. Buch; Pompeckj, p. 280.
1898 *Pecten personatus* Goldfuss; Greppin, p. 128.
1898 *Pecten (Amusium) andium* sp. nov; Tornquist, p. 31.
1903 *Pecten (Amusium) personatus* Goldfuss; Burckhardt, p. 22, pl. 2, fig. 7.
1907 *Pecten pumilus* Lamarck; Deninger, p. 453.
1910 *Amusium pumilus* (Lamarck); Lissajous, p. 363, pl. 10, figs. 11, 12.
1912 *Pecten (Variamussium) pumilus* Lamarck; Dal Piaz, p. 246, pl. 1, fig. 14.
1916 *Variamussium pumilum* (Lamarck); Paris and Richardson, p. 529.
1916 *Pecten pumilus* Lamarck; Borissiak and Ivanoff, p. 50, pl. 3, figs. 17, 18.
1920 *Pecten (Chlamys) Agathis* Gemmellaro; Dareste de la Chavanne, p. 51.
1923 *Pecten (Amussium) personatus* Goldfuss; Jodot, p. 136, pl. 40, fig. 11a.
1923 *Pecten (Variamussium) pumilus* Lamarck; Ernst, p. 55.
1924 *Pecten (Variamussium) personatus* Goldfuss; Hennig, p. 17, pl. 2, figs. 3–6.
1926 *Variamussium pumilum* (Lamarck); Staesche, p. 84.
1926 *Chlamys amalthei* (Oppel); Staesche, p. 62.
1929 *Pecten (Amussium) pumilus* Lamarck; Lanquine, p. 132, 188.
1936 *Variamussium pumilum* (Lamarck); Cox, p. 19, pl. 1, fig. 18.
1936 *Variamussium pumilus* (Lamarck); Dechaseaux, p. 65.
non 1938 *Variamussium pumilum* (Lamarck); Weir, p. 50, pl. 3, fig. 21.
1950 *Variamussium pumilum* (Lamarck); Channon, p. 248.
1965 *Amussium pumilum* (Lamarck); Dahm, p. 29.
1966 *Variamussium pumilum* (Lamarck); Behmel and Geyer, p. 28.
non 1973 *Chlamys (Acquipecten) amalthea* (Oppel); Lentini, p. 27, pl. 15. fig. 9.
1974 *Propeamussium (Parvamussium?) geelvinki* sp. nov; Skwarko, p. 80, pl. 26, figs. 2, 3.
1977 *Paramussium pumilus* (Lamarck); Dietl, pl. 2, fig. 3.
1978 *Parvamussium pumilus pumilus* (Lamarck); Hölder, p. 4, pl. 5, fig. 6, text figs. 1–3.
1978 *Parvamussium pumilus atlasense* subsp. nov; Hölder, p. 7, pl. 1, figs. 1–5, text fig. 4.
1978 *Parvamussium personatum* (Goldfuss); Hölder, p. 9, pl. 1, figs. 6–9, pl. 2, figs. 1–4, pl. 4, figs. 1–6, text figs. 1, 5, 7 (pars), 8.
? 1978 *Parvamussium* aff. *personatum* (Goldfuss); Hölder, p. 20, pl. 5, figs. 1–4, text fig. 11.
? 1978 *Parvamussium dumortieri* sp. nov; Hölder, p. 22, pl. 4, fig. 7.

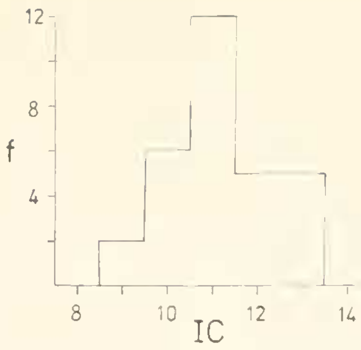
Lectotype of *Pecten pumilus* Lamarck 1819, p. 183 designated by Hölder, 1978, p. 4, text fig. 2a; MN unnumbered; H: 6.1, L: 5.5; ?Toarcian, Swabia (Hölder, 1978); one of five syntypes preserved in MN.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

'P. testa minima, rotundata-ovata radiis 10 ad 12.'

2. AMENDED DIAGNOSIS

Distinguished from *P. (P.) laeviradiatum* by the larger modal number of internal costae, relatively insignificant dorsal extension of the auricles beyond the hinge-line and by the finer and more numerous costae on the left valve. Distinguished from *P. (P.) nonarium* by the lack of intercalary internal costae and by the termination of the internal costae somewhat closer to the ventral margin.



Text fig. 9: *Propeamussium (P.) pumilum* – frequency distribution for number of internal costae.

3. AMENDED DESCRIPTION

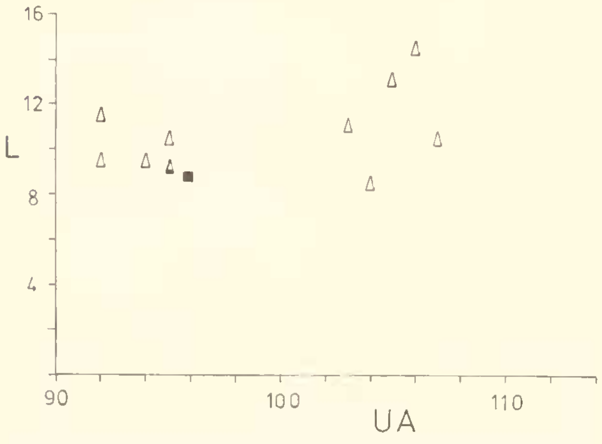
Disc sub-ovate, higher than long at all sizes, maximum height 42 mm (Dumortier, 1874). Umbonal angle very variable (text fig. 10) increasing slightly during ontogeny. Disc flanks low.

Equilateral, equivalve, low convexity.

Intersinal distance greater in left valve than right. Small byssal notch becoming relatively smaller during ontogeny.

Auricles well demarcated from disc, moderate in size, anterior slightly larger than posterior. Dorsal margin of right anterior auricle extended slightly beyond hinge line. Posterior auricles meeting hinge line at an obtuse-right angle, anterior auricles meeting hinge line at an acute-right angle. Anterior auricle of right valve meeting disc at a right angle, other auricles meeting disc at an acute angle.

Shell thin. Shell structure consisting of a maximum of 5 layers (Hölder, 1978) with the fourth and fifth developed only on the left valve. Innermost layer (layer 1) of comarginally orientated crystallites overlying radially orientated crystallites of layer 2, which is locally thickened to form radial costae, 9–13 in number (text fig. 9), terminating at about 5/6 total height. Layer 3 of similar structure locally thickened to form comarginal striae. Layers 4 and 5 composed of unordered crystallites locally thickened to form a reticulate ornament with intercalary striae, closer in layer 5.



Text fig. 10: *Propeamussium (P.) pumilum* – length/umbonal angle.

4. DISCUSSION

Hölder (1978) has recently located five syntypes of '*P.*' *pumilus* Lamarck (MN) and shown them to be typical representatives (with 11 internal costae) of the species with 9–13 internal costae described in section 3. '*P.*' *paradoxus* Münster is simply representative of the less common variants with up to 13 internal costae. '*P.*' *personatus* Goldfuss was said to include forms with up to 14 internal costae but since the type material was destroyed in the 2nd. World War, this cannot be confirmed. Hölder's (1978) opinion that Münster's species (from the Toarcian) and Goldfuss's species (from the Aalenian) can be distinguished by the lack of a byssal notch, equality of the auricles, lack of dorsal extension of the anterior auricle of the right valve and perpendicular posterior margin of the posterior auricle in the former species is not vindicated by the original figures. Neither does there seem to be any material evidence to support Hölder's claim amongst the generally incompletely preserved syntypes of '*P*'. *paradoxus* (GPIB 611b, 611c; e. g. Pl. 1, figs. 3, 9). Hölder's distinction of Toarcian from Aalenian forms on the basis of UA (105°–120° cf. 90°–100°) is invalid since Staesche (1926) cites a Toarcian specimen with UA: 96°. On his own admission slight differences in shell structure may well be due to imperfect preservation.

The author has been unable to trace the original descriptions of '*P.*' *intusradiatus* Münster, '*P.*' *intusstriatus* Münster and '*P.*' *contrarius* v. Buch but Hölder has figured one of the syntypes (HM) of the latter, showing it to be indistinguishable from *Propeamussium (P.) pumilum*, and included the others in synonymy with Lamarck's and Goldfuss' species. Weir's (1938) record of '*Variamussium*' *pumilum* is however more reminiscent of *Radulopecten vagans* while Morris and Lycett's (1853) record of '*Pecten*' *personatus* from the Bathonian has been shown by Cox and Arkell (1948) to refer probably to specimens of *Camptonectes*.

The syntypes of '*P*'. *amalthei* Oppel (BSPHG) are very poorly preserved but one specimen (BSPHG AS VIII 166; Pl. 1, Fig. 8) shows 10 clear internal costae which, combined with the characteristic left valve exterior ornament, leaves little doubt that it should be included in *P. (P.) pumilum*. Stoliczka's (1861) record of Oppel's species is almost certainly a misnomer for *Chlamys (Ch.) textoria* while Lentini's (1973) record resembles *Ch. (Ch.) pollux*. '*P.*' *Agathis* Gemmellaro was said to be close to Oppel's species and the description of asymetric right and left valve ornament confirms the similarity.

'*P.*' *Dumortieri* Jaubert was erected without diagnosis for an unfigured specimen from Var (Provence) designated as '*P.*' *personatus* by Dumortier. It was said to resemble the latter in its internal costation and seems likely to have been one of the typically large specimens of *P. (P.) pumilum* frequently recorded from Var. Hölder's use of *dumortieri* for a specimen (MHNL 9075) referred to '*P.*' *pumilus* by Dumortier (1874) must now be rejected as a secondary homonym in *Propeamussium*. The specimen may however be worthy of a specific distinction on account of its UA (more than 125°).

'*P.*' *penninicus* Neumayr from the Oxfordian resembles *P. (P.) pumilum* in apparently having 11 internal costae but differs in the unusually strong reticulate ornament on the left valve. Hölder (1978), who has studied the types in Vienna, considers however that this may be due to abrasion and refers another similar specimen from the same stage to *'Parvamussium'* aff. *personatum*.

'P'. undenarius Quenstedt and *P. ('Pa'?) geelvinki* Skwarko with 11 and 12 internal ribs respectively show no obvious differences from *P. (P.) pumilum* and while *'P.' Paronae* De Gregorio is only known from two specimens, both less than 5 mm in height, there can be little doubt as to the affinities of the species. *'Pa.'* sp. Hölder is only distinguished by its low UA (90°) which by the evidence of the figure seems to be the result of abrasion.

'P.' ('Amusium') andium Tornquist was based on specimens collected and referred to *'P.' pumilus* by Gottsche (1878) which were said to differ from the latter species by the lack of radial ornament. It seems highly likely that they were merely the right valves of *P. (P.) pumilum*.

Mention of 11 internal costae in the original description of *'P.' incrustatus* Defrance strongly suggests that the species is synonymous with *P. (P.) pumilum*.

5. STRATIGRAPHIC RANGE

P. (P.) pumilum is recorded from the U. Pliensbachian of England (BM L94170–3, SM J42033), France (Lanquine, 1929), Germany (Brauns, 1971; Oppel, 1853), Sicily (Gemmellaro, 1874), Algeria (Dareste de la Chavanne, 1920), Chile (Möricke, 1894), and Spain (Behmel and Geyer, 1966). The latter authors also record the species as occurring rarely in the L. Pliensbachian but since there are no supporting figures, some doubt must remain. Other than in the U. Pliensbachian of E. Spain and Sicily, *P. (P.) pumilum* is rare before the Toarcian. The species is thereafter locally common until the L. Bajocian but definite U. Bajocian records are completely lacking. Bathonian records are limited to Dechaseaux (1936), Deninger (1907) and Dal Piaz (1912) but only the latter produces unequivocal evidence of a Bathonian specimen in the form of a figure. Greppin's (1898) record from the 'Grande Oolithe' of Switzerland was re-assigned to the Sauzei zone (L. Bajocian) by Staesche (1926) and Morris and Lycett's (1853) record from the Great Oolite was shown by Cox and Arkell (1948) to be unsupported by any material corresponding to their description (see Section 4). It is clear that *P. (P.) pumilum* is a rare species after the L. Bajocian and occurrences after the Bathonian are limited to two equivocal specimens from the Oxfordian of the Balkans (Neumayr, 1871) and a further one from the same stage in Swabia (Hölder, 1978).

6. GEOGRAPHIC RANGE

P. (P.) pumilum is widespread in Europe (text fig. 11) and on a world scale spans a palaeolatidudinal range of about 40° (text fig. 12). Although very cosmopolitan the species is not known worldwide, contrary to the opinion of Staesche (1926). There are notable absences in the L. Jurassic of Australasia and western N. America despite the widespread development of appropriate sedimentary facies (see Section 8) in these regions. Yet, wherever *P. (P.) pumilum* arose, migration must have occurred between Europe and S. America during the L. Jurassic to explain the observed distribution but the most obvious migration routes (via N. America/Arctic, and via the W. Pacific) are precluded because of the lack of fossil evidence en route. Hallam (1973) considered that the distribution of the aberrant pectinid *Weyla*, restricted to the western margins of the Americas in the L. and M. Lias but also occurring in the Ethiopian Province in the U. Lias, indicated the development of a marine connection between Argentina, Antarctica and S. America in the Toarcian. The distribution of the ammonite *Bouleiceras*, restricted to the Ethiopian Province and S. America in the L. Toarcian (Hillebrandt, 1973) supports such a view and it seems also to provide a good explanation for the distribution of *P. (P.) pumilum*. However, occurrences of the species in the M. Lias of both Chile (Möricke, 1894) and Europe indicate that a marine connection was established at least by the U. Pliensbachian while occurrences of *Weyla* in the Jamesoni zone of Spain (Dubar, 1925) indicate a seaway in the L. Pliensbachian.

Damborenea and Manceñido (1979) consider that the latter occurrences in fact indicate the existence of a direct marine connection (through central America) during the Lias.

Text fig. 11: *Propeamussium (P.) pumilum* – European distribution.

During the Bajocian *P. (P.) pumilum* extended its range along the southern margins of Tethys but was still unable to penetrate Asia or western N. America despite the undoubted development of a marine connection between the latter and Europe by this time (Hallam, 1975a). This strongly suggests an ecological exclusion and the aviculopectinid *Otapiria*, restricted to the Pacific region (Hallam, 1977) and occurring in comparable facies, may have competitively restricted *P. (P.) pumilum*.

The broad distribution of *P. (P.) pumilum* provides some support for the view (see Section 8) that the species may have had a pseudo-planktonic mode of life.

Text fig. 12: *Propeamussium (P.) pumilum* – World distribution (Pliensbachian reconstruction).

7. DESCRIPTION OF ECOLOGY

P. (P.) pumilum first occurs commonly in U. Pliensbachian marls in E. Spain and Sicily where it occurs with *Lima*, *Oxytoma* and *Placunopsis* together with abundant brachiopods, gastropods and cephalopods. It subsequently becomes very abundant at certain horizons in the L. Toarcian bituminous shales (Posidonienschiefer) of S. W. Germany, notably above the Oberer Stein at Göppingen where it forms a shell bed. The associated fauna is largely restricted to abundant *Bositra bronni* and *Pseudomytiloides dubius* together with ammonites and belemnites. The maximum height of 9.5 mm (GPIT) is less than in contemporaneous deposits in N. Germany (Staesche, 1926) while specimens from Var (Provence) reach a height of 42 mm (Dumortier, 1874).

The species is less common in the U. Toarcian but occurs in the condensed sands and ironstones of Lower Saxony (Ernst, 1923).

In the Opalinum zone (Aalenian) *P. (P.) pumilum* occurs fairly commonly in the Northampton Sand Ironstone, a chamosite oolite, in association with a diverse bivalve fauna including *Camptonectes (C.) auritus*, *Eopecten abjectus*, *Entolium*, *Lima*, *Gervillia*, *Myophorella*, *Ceratomya* and *Astarte*. Subsequently it occurs commonly in the Murchisonae zone of S. Germany which is developed in the same facies. Goldfuss' synonym has provided a name for one terrigenous intercalation into the sequence of Aalen (the Personatensandstein) where *P. (P.) pumilum* crowds the bedding planes to the virtual exclusion of other fossils. The maximum height attained is 16 mm (GPIT).

In the Aalenian of the Cotswolds *P. (P.) pumilum* occurs sporadically in all the oolitic horizons. In the Murchisonae zone at Cornwell (Oxon.) it is found very abundantly in a low diversity shell bed (Sylvester-Bradley, 1968). In the L. Bajocian of the same region it locally forms shell beds in the Notgrove Freestone.

P. (P.) pumilum is not known to be common elsewhere and it is conspicuously rare in the deep water pelagic limestones of the peri-Mediterranean region.

It is clear from the foregoing that there is an inverse correlation between the abundance of *P. (P.) pumilum* and the diversity of the associated fauna. It is however found in a wide variety of sedimentary facies although *P. (P.) laeviradiatum* is a rare associate. Most accumulations of *P. (P.) pumilum* consist of disarticulated valves but the incidence of abrasion and breakage is low enough to suggest minimal transport from the life position.

8. INTERPRETATION OF ECOLOGY

P. (P.) pumilum forms part of the faunal association which characterises laminated bituminous shales (Hallam, 1976) and whose low diversity is thought to be indicative of anaerobic or near-anaerobic conditions close to the sea floor. The principle formation of this type in which *P. (P.) pumilum* occurs (the Posidonienschiefer) is dominated by the bivalves *Bositra* and *Pseudomytiloides* together with ammonites and belemnites. The last two were almost certainly planktonic and thus independent of bottom conditions. *Pseudomytiloides* is frequently found in large numbers around driftwood to which *Pentacrinus* is also attached (Hauff, 1953) and it has been suggested that the inoceramid gained independence of the sea floor by adopting a byssate, pseudoplanktonic mode of life. Floating seaweed is invoked as a substrate to explain accumulations of *Pseudomytiloides* in the absence of driftwood. A planktonic mode of life has also been suggested for *Bositra* (Jefferies and Minton, 1965) based largely on its independence of sedimentary facies and presence in areas where benthos is sparse, such as euxinic black shales and deep water pelagic limestones. Jefferies and Minton favour a genuinely planktonic, rather than pseudoplanktonic, mode of life for *Bositra*, owing to the lack of shell features indicative of byssal attachment. The association of *P. (P.) pumilum* with this supposedly planktonic fauna has led to a persistent belief among German palaeontologists (dating back to Hauff, 1921) that this species was likewise planktonic. Hauff considered that *P. (P.) pumilum* was byssate and thus if epibenthic at the mercy of fluctuating bottom conditions. He therefore concluded that it must be pseudoplanktonic in the Posidonienschiefer, ignoring the fact that byssate pectinids may still unattach themselves and escape from locally unfavourable bottom conditions by swimming. Staesche (1926) also considered that the smaller size of specimens from the Posidonienschiefer was a reflection of byssal attachment to floating seaweed, with the implication that the byssus was only strong enough to support small individuals. However, Recent byssally suspended pectinids (e. g. *Gloripallium pallium)* commonly reach a height of 60 mm (Waller, 1972b) and it seems much more likely that small size in the Posidonienschiefer was the result of oxygen deficiency, all the bivalves being less than 30 mm in height. At present it cannot be said whether low oxygen tension directly caused stunting or simply led to high juvenile mortality.

A. Seilacher (pers. comm., 1977) reports that *P. (P.) pumilum* has been found associated with driftwood but the author's field observations provide no confirmation of this. More telling evidence against a pseudoplanktonic mode of life is provided by the rarity of *P. (P.) pumilum* in the deep water pelagic limestones in which *Bositra* is common. This is contrary to expectation for a pseudoplanktonic bivalve and it is the author's impression that unlike *Bositra* and *Pseudomytiloides, P. (P.) pumilum* does not occur uniformly throughout the Posidonienschiefer but is concentrated at a few levels, suggesting a dependence upon bottom conditions. Hallam (1976) has emphasised that truly anaerobic conditions may only have existed within the sediment and that just above the sediment/water interface there was occasionally enough oxygen to support a eurytopic fauna. Indeed truly epibenthic organisms *(Pseudodiadema* and rhynchonellid and discinid brachiopods) are known from the Posidonienschiefer and Kauffman (1978) has now made the suggestion that even *Bositra* and *Pseudomytiloides* may have lived on or only slightly above the sea floor.

There is no evidence for a pseudoplanktonic mode of life in living *Propeamussium*. Knudsen (1967) reports both pelagic and benthonic organisms in the stomach contents of *P. sibogai* and considers that the pelagic fraction was probably captured during swimming activity. Most of the known species have been dredged from the sea bed in the bathyal and abyssal zones and appear to have been free living rather than byssate when adult (Knudsen, 1967, 1970). Waller (1971) reports no trace of a pedal retractor muscle scar in extant species. The only Recent pectinid known to have a pseudoplanktonic mode of life is *Leptopecten latiauritus monotimeris* (see Clark, 1971). It resembles *P. (P.) pumilum* in its small size but differs in its strong prosogyrous inclination, a feature considered to be characteristic of a loosely suspendes mode of life (Kauffman, 1969).

It may therefore be concluded from the foregoing that *P. (P.) pumilum* was epibenthic and unattached for most of its life and able to live on a wide variety of substrates under variable conditions of oxygen tension and turbulence. Its particular abundance in association with low diversity faunas indicates an opportunistic adaptive strategy (Levinton, 1970). Mutual exclusion from *P. (P.) laeviradiatum* (see p. 31) may have been due to competition.

The large size of specimens from Var compared to those from more northerly palaeolatitudes may be the result of enhanced growth rates due to increased temperature, as has been observed in Recent bivalve species on approaching the equator (Nicol, 1967). Such an effect coupled with the pattern of ontogenetic increase in the number of radial striae could account for the relatively coarse ornament in large specimens from Morocco (Hölder, 1978).

9. FUNCTIONAL MORPHOLOGY

The small adult size, thin shell, low convexity, subdued ornament, ontogenetic decrease in the relative size of the byssal notch and ontogenetic increase in the umbonal angle place *P. (P.) pumilum* close to a paradigm for a short byssate juvenile phase followed by a reclining/swimming phase in a low energy environment. Such a mode of life is well in accord with the palaeoecology of the species in such deposits as the Posidonienschiefer. The species appears to have been less well adapted to the higher energy environments in which it occurs (e. g. cross bedded oolites and sandstones) but was presumably able to survive frequent burial and disturbance by the swimming response.

10. ORIGINS AND EVOLUTION

If it is assumed (see p. 32) that *P. (P.) laeviradiatum* is the descendant of *P. (P.) pumilum* (rather than vice versa) then there remain no plausible ancestors for *P. (P.) pumilum* in the Jurassic. The U. Palaeozoic genus *Pernopecten* seems, by the evidence of shell structure, to be the ultimate source of Mesozoic *Propeamussium* (Waller, 1971).

There are no obvious phyletic trends in *P. (P.) pumilum*. Specimens derived from the same limestone facies (to rule out ecophenotypic variation) show a phyletic reduction in maximum height from 42 mm in the L. Toarcian (Dumortier, 1874) to 23 mm in the Aalenian (OUM J14491) to 18 mm in the L. Bajocian (YM 502) but these specimens also lie on a S-N line (from respectively S. France to S. England to N. England) so it is possible that a latitudinal temperature gradient may be the causal factor (see Section 8). However, a phyletic reduction in maximum height would be concordant with the evidence from eurytopy and opportunism which indicates the general prevalence of 'r' selection (Gould, 1977).

No convincing deterministic explanation is available for the post L. Bajocian decline of *P. (P.) pumilum*.

Propeamussium (Propeamussium) laeviradiatum (Waagen 1867)

Pl. 1, Figs. 5, 6, 10, 12; text figs. 13–17

Synonymy

v* 1867 *Pecten laeviradiatus* sp. nov.; Waagen, p. 633, pl. 31, figs. 4a, 4b.

1883 *Pecten cornutus* Quenstedt; Whidborne, p. 498, pl. 16, figs. 1, 2, 2a (non Quenstedt sp).

1883 *Pecten laeviradiatus* Waagen; Whidborne, p. 500.

v* 1883 *Pecten fenestralis* sp. nov.; Whidborne, p. 500.

1886 *Pecten (Amusium) subpersonatus* sp. nov.; Vacek, p. 111, pl. 19, figs. 5, 6.

1886d *Pecten Animensis* sp. nov.; De Gregorio, p. 21, pl. 13, figs. 8, 10–12, 16.

1893 *Pecten (Amusium) subpersonatus* Vacek; Botto-Micca, p. 174.

1898 *Pecten dionvillensis* sp. nov.; Benecke, p. 25, pl. 1, fig. 4.

1916 *Variamussium fenestrale* (Whidborne); Paris and Richardson, p. 528.

v 1916 *Variamussium laeviradiatum* (Waagen); Paris and Richardson, p. 528, pl. 44, figs. 1a–c.

v 1926 *Variamussium laeviradiatum* (Waagen); Staesche, p. 86, pl. 6, figs. 8, 9.

1929 *Pecten (Amusium) laeviradiatus* Waagen; Lanquine, p. 200.

? 1942 *Pecten (Variamussium) coloradoensis* Weaver; Leanza, p. 176, pl. 7, figs. 3, 5, pl. 10, fig. 3.

(?) 1959 *Variamussium babunokawense* Kimura; Tamura, p. 60, pl. 6, figs. 20–22.

(?) *1961* *Propeamussium babunokawensis* (Kimura); Hayami, p. 255.

? 1972 *Parvamussium (Parvamussium) donaiense* Mansuy; Hayami, p. 197, pl. 34, figs. 11, 12, pl. 38, figs. 6, 7.

1978 *Varientolium* cf. *laeviradiatum* (Waagen); Hölder, p. 23, text fig. 10d, pl. 3, fig. 6.

Lectotype of *Pecten laeviradiatus* Waagen 1867, p. 633, pl. 31, figs. 4a, 4b designated herein; BSPHG AS XXII 29; Pl. 1, Fig. 5 herein; Bajocian, 'Sowerbyi' zone (Discites-Laeviuscula zones); Gingen, Württemberg. Paralectotypes; the 3 other syntypes (BSPHG); also 'Sowerbyi' zone, Gingen.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

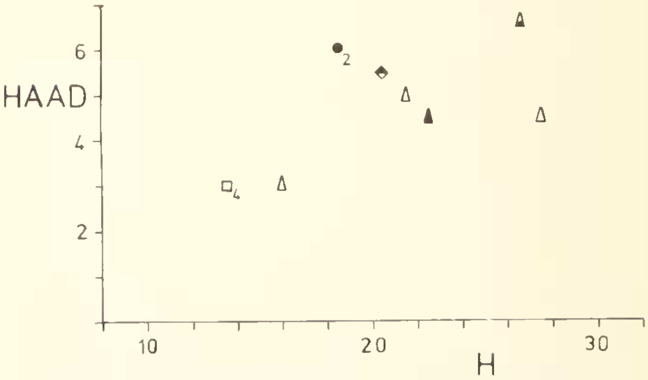
‚Flachgewölbte Schalen, beide Klappen gleich, auf denen vom Wirbel sieben scharfe mit senkrechten Seiten abfallende Rippen ausstrahlen. In gewissen Entfernungen vom Wirbel setzen sich anfangs haarfein, dann stärker werdend, genau die Mitte zwischen den vorhergehenden haltend, neue Rippen ein, und so mehrmals, so daß man am Rande 30 und mehr Strahlenrippen zählen kann. Diese Rippen haben auf ihrem Rücken eine von Kanten begrenzte ebene Fläche, die vollkommen glatt, ohne eine Spur von Anwachsstreifen ist. Auf den ganz flachen Zwischenräumen aber bemerkt man äußerst feine concentrische Anwachsstreifen. Der Steinkern ist durchaus glatt.

Nicht selten und sehr bezeichnend für die Zone des *Amm. Sowerbyi* von Pommer (Franken), Gingen (Württemberg), Aselfingen (Baden), Betzenau und Schambelen (Canton Aargau).

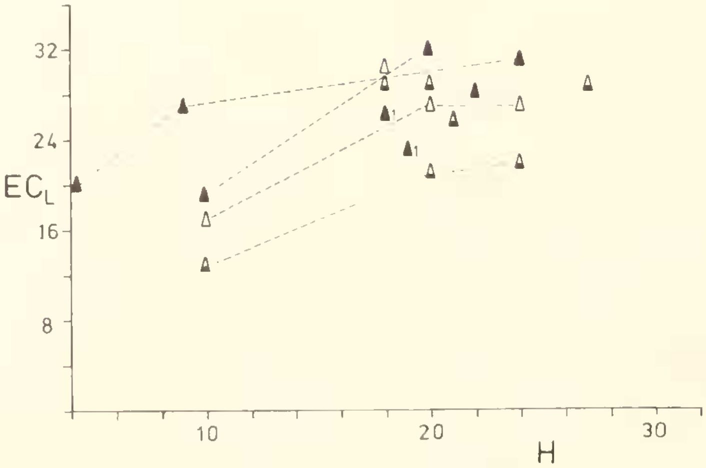
Scheint im Pariser, Nordenglischen und Norddeutschen Becken zu fehlen.'

2. AMENDED DIAGNOSIS

Distinguished from all other species of *P. (Propeamussium)* by the horn-like dorsal extensions of the right valve auricles and by the generally coarser ornament.



Text fig. 13: *Propeamussium (P.) laeviradiatum* – height of anterior auricle dorsal of hinge line/height.



Text fig. 14: *Propeamussium (P.) laeviradiatum* – number of external costae on left valve/height.

3. AMENDED DESCRIPTION

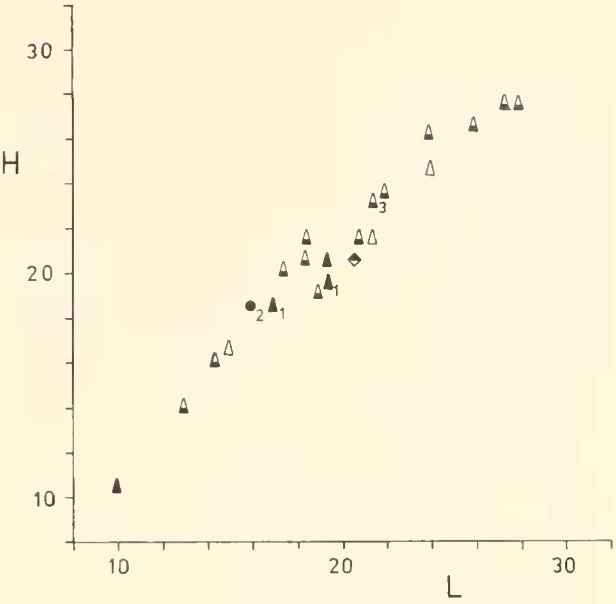
Essentially similar to *P. (P.) pumilum* but differing by the diagnostic horn-like auricles (Pl. 1, Fig. 12) which increase in height from about 3 mm (H: 10) to 6 mm (H: 28), maximum 6.5 mm (text fig. 13). Also differing in the tendency to develop a sub-orbicular disc (text fig. 15) near the maximum height of 30 mm (BM L42019), in the slightly smaller mean L/UA (text fig. 16), in the smaller modal number of internal costae (9, range 9–10) and in the less numerous radial costae on the left valve (13–27 at H: 10, increasing by intercalation to a maximum of 37 at H: 30 [text fig. 14]) which sometimes form a reticulate pattern with the comarginal striae (Pl. 1, Fig. 6). The shell is somewhat more robust than that of *P. (P.) pumilum* but still fairly thin.

4. DISCUSSION

The earliest available name for the species described in Section 3 is *'Pecten' laeviradiatus* Waagen. Although the four syntypes (BSPHG), all left valves, are seen only from the exterior there can be no doubt that they possess the internal costae of the species described above; external costation and metric proportions (1) are within the range of the latter. A lectotype (BSPHG AS XXII 29; Pl. 1, Fig. 5) is herein designated.

Whidborne (1883) thought that the smooth right valves of *Propeamussium (P.) laeviradiatum* belonged to a separate species and referred them to *'Pecten' cornutus* Quenstedt (1858). It was the present author's previous opinion (Johnson, 1980) that the single known type of Quenstedt's species (from the Oxfordian) is in fact a late representative of *P. (P.) laeviradiatum*. However, re-examination of the specimen (GPIT 4–74–10; Pl. 1, Fig. 11) has failed to confirm the existence of the internal costae previously thought to have been present and while metric proportions (2) are largely indistinguishable from *P. (P.) laeviradiatum* it now seems likely that the specimen is an example of *Entolium*. Nevertheless other specimens with internal costae and left valve ornament identical to that of *P. (P.) laeviradiatum* are known from the U. Jurassic. *'Variamussium' habunokawense* Kimura; Tamura from the U. Jurassic of Japan seems indistinguishable from *P. (P.) laeviradiatum* but since the stratigraphic horizon (cf. Section 5) is so high and it is not yet clear whether the characteristic dorsally extended right valve auricles of *P. (P.) laeviradiatum* are present it is perhaps unwise to assume that this form is conspecific. Kimura's original description has proved impossible to trace.

'P.' fenestralis Whidborne was separated from *'P.' laeviradiatus* on the basis of strong comarginal ornament on the left valve and a larger number of internal costae. However Waagen's original description in fact specifies comarginal ornament. Museum specimens show a variable development of this feature (Pl. 1, Figs. 5, 6) and it seems likely, as indeed Whidborne suggested, that this is due to differing amounts of post-mortem abrasion. Whidborne's figured specimen of *'P.' fenestralis* (SM J4758) is seen only from the exterior and there is no other appropriately preserved material to evidence Whidborne's claim of up to 12 internal costae in this species. *'P.' fenestralis* is also inseparable by its metric proportions (3).



Text fig. 15: *Propeamussium (P.) laeviradiatum* – height/length.

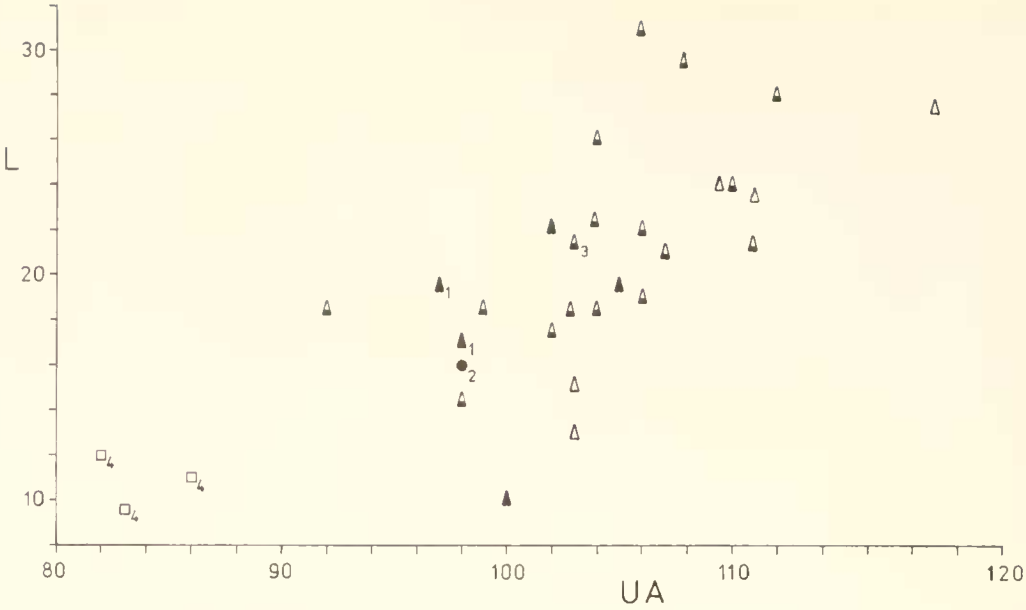
'P.' ('Amusium') subpersonatus Vacek was said to possess only 7 internal costae. However, these could only be seen through the right valve and so the number may be an underestimate. The left valve exterior ornament is identical to that in *Propeamussium (P.) laeviradiatum*. Dorsally extended auricles are absent in the figured specimen but this is clearly due to breakage.

'P.' Animensis De Gregorio was erected for specimens which Vacek referred to *'P.' ('Amusium') subpersonatus* but of which only the exterior of the left valve was visible. The ornament is however identical to that of *P. (P.) laeviradiatum*. Similarly, *'P.' dionvillensis* Benecke can be assigned to the latter species even though only the exterior of the left valve is figured.

It has been impossible to trace the original description of *'P.' ('Variamussium') coloradoensis* Weaver but Leanza's (1942) description of the latter, specifying 13–19 external costae increasing by intercalation and an umbonal angle of 105–115°, is indistinguishable from *P. (P.) laeviradiatum*. However, the figures do not reveal any sign of the horn-like auricles and this fact together with the anomalously early stratigraphic horizon (Oxynotum zone) casts doubt on the affinity of *'P.' ('V.') coloradoensis* with *P. (P.) laeviradiatum*. The original description of *'Parvamussium' ('Pa.') donaiense* Mansuy is also untraceable. Hayami's (1972) description of the species from the Toarcian of Vietnam specifies that the only difference from *P. (P.) laeviradiatum* is the presence of fewer (7 or 8) internal costae. In the absence of sufficient material to make an adequate assessment of variation in this character it is impossible to judge whether such forms should be accorded specific status. They may merely be geographic variants.

5. STRATIGRAPHIC RANGE

Apart from a dubious record from the Sinemurian (see Section 4), the earliest record of *P. (P.) laeviradiatum* is a single specimen (BM LL1579) from the U. Pliensbachian of Vieux-



Text fig. 16: *Propeamussium (P.) laeviradiatum* – length/umbonal angle.

pont (Normandy). Only one museum specimen (BM unnumbered, from Beaminster, Dorset) is known from the Toarcian but Whidborne (1883) records the species from the U. Toarcian of Yeovil, Somerset where the appropriate facies (see Section 8) are well developed. Hayami (1972) records a closely related, if not conspecific form (see Section 4), from the Toarcian of Vietnam.

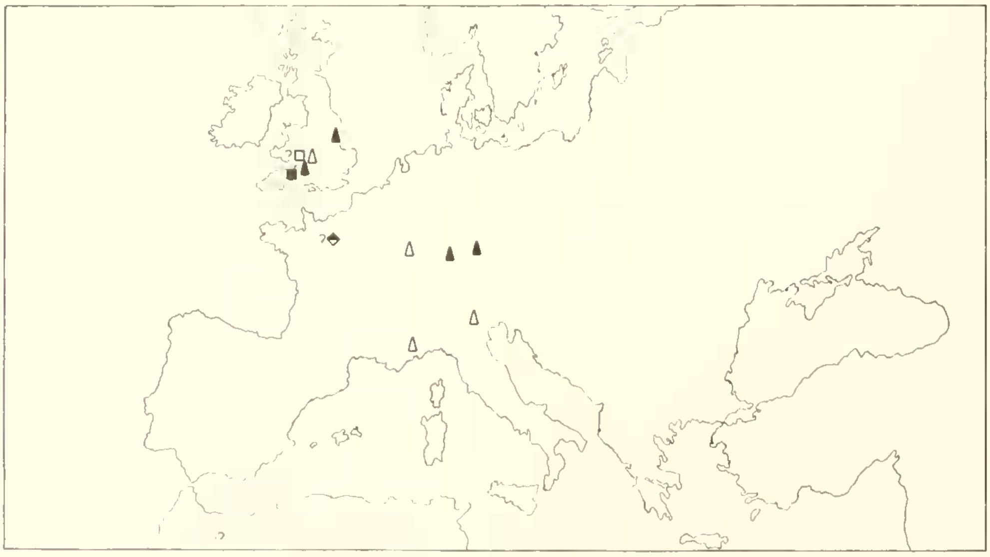
P. (P.) laeviradiatum is locally common in the Aalenian and in the Bajocian until the Laeviuscula zone (L. Bajocian). There are no records from the U. Bajocian and Bathonian records are limited to 3 specimens (BM L97035-7) from Stroud, Gloucestershire whose HAAD/H (4) is inseparable from *P. (P.) laeviradiatum*, but whose high L/UA may imply a specific distinction. Specimens from Japan referred to by Tamura (1959) and Hayami (1961) may constitute records from the U. Jurassic (see Section 4).

6. GEOGRAPHIC RANGE

P. (P.) laeviradiatum occurs sporadically over a large part of the European region (text fig. 17). Its distribution is almost certainly related to the localised development of appropriate sedimentary facies (see Section 8). Material from Argentina (Leanza 1942), Vietnam (Hayami 1972) and Japan (Tamura 1959, Hayami 1961) may evince an extra-European distribution (see Section 4).

7. DESCRIPTION OF ECOLOGY

In Europe *P. (P.) laeviradiatum* first occurs commonly in condensed sandy limestones of the Opalinum zone in Dorset, where it attains a maximum height of 30 mm (BM L42019). The associated benthic fauna is dominated by the bivalves *Pseudopecten (Echinopecten) barbatus*, *Eopecten*, *Ctenos-*



Text fig. 17: *Propeamussium (P.) laeviradiatum* – European distribution.

treon, Neocrassina and *Placunopsis* and the gastropod *Pseudomelania* together with abundant brachiopods of the form genera '*Rhynchonella*', '*Terebratula*' and '*Zeilleria*'. *P. (P.) laeviradiatum* also occurs in a similar sedimentary and faunal association, albeit somewhat less commonly, in the Murchisonae and Concavum zones of S. England. It is, however, absent from the Northampton Sand Ironstone (Opalinum zone) where *P. (P.) pumilum* and *Entolium (E.) corneolum* are common.

P. (P.) laeviradiatum is recorded commonly with *Ps. (Ec.) barbatus* in the Aalenian sandy limestones of Provence (Lanquine, 1929) but is absent from the Aalenian of S. Germany where the stage is developed in sands and shales overlain by chamositic ironstones containing abundant *P. (P.) pumilum* and *E. (E.) corneolum*. However, in the L. Bajocian of S. Germany *P. (P.) laeviradiatum* is found commonly in the Sowerbyi-Banke (Discites and Laeviuscula zones) where it reaches a maximum height of 22.5 mm (GPIT). The sediments are condensed marly oolites containing a diverse bivalve fauna but few ammonites. In limonitic sandy limestones of equivalent age in the Bristol district *P. (P.) laeviradiatum* is also common in association with an abundant and diverse fauna of ammonites, bivalves and brachiopods.

The only records from the peri-Mediterranean region are from Provence (see above) and the Aalenian of the Italian Alps (Botto-Micca, 1893; De Gregorio, 1886d; Vacek, 1886) where the sediments are condensed limestones, probably formed on a submarine rise. The associated fauna consists of abundant ammonites and brachiopods, small gastropods and more rarely the bivalves *Ps. (Ec.) barbatus, E. (E.) corneolum* and *Eopecten*.

8. INTERPRETATION OF ECOLOGY

The coarse – grained condensed deposits in which *P. (P.) laeviradiatum* occurs most commonly are indicative of high energy conditions with a low sediment input. The occasional presence of locally derived conglomerates (e. g. Opalinum zone in Dorset) indicates active erosion while limonitic overgrowths suggest periods of non-deposition. The fauna associated with *P. (P.) laeviradiatum* exhibits a range of adaptations for achieving stability in high energy conditions. *Ps. (Ec.) barbatus* possesses a strongly spinose right valve which probably served to grip the sediment and prevent current scour (see p. 83). *Eopecten* has an exceptionally deep byssal notch which indicates that byssal fixation could have been maintained throughout ontogeny. *Ctenostreon* has a thick shell whose weight would have resisted overturning by currents. The terebratulid and rhynchonellid brachiopods were all attached by means of a pedicle which probably performed the same stabilising function as the byssus in *Eopecten*. Contrary to Rudwick's (1970) opinion, Thayer (1975) has shown that the pedicle attachment strengths of both terebratulid and rhynchonellid brachiopods compare favourably with byssate bivalves and are sufficient to anchor the animal in very high energy environments. The paucity of infauna in deposits containing *P. (P.) laeviradiatum* may be due to the difficulty of avoiding exhumation by current scour.

P. (P.) laeviradiatum is rarely found with the closely related eurytopic species *P. (P.) pumilum* nor is the morphologically similar pectinid *Entolium (E.) corneolum* a common associate. However, both of the latter species occur in condensed chamosite oolites whose depositional environment (high energy, low siliciclastic input) would appear to have been ideal for *P. (P.) laeviradiatum*. The absence of *P. (P.) laeviradiatum* from such facies is therefore strongly suggestive of competitive exclusion by either or both of *P. (P.) pumilum* and *E. (E.) corneolum*. This factor together with an intolerance of high rates of sedimentation probably accounts for the lack of *P. (P.) laeviradiatum* in S. Germany before the Bajocian. The rarity of the species in the peri-Mediterranean region is clearly due to the widespread development of low energy, pelagic limestone facies.

Most modern species of the morphologically similar genus *Amusium* live in the deep sea (Knudsen, 1967) but at least two *(A. pleuronectes* and *A. japonicum)* are known to migrate into shallow water for the purpose of spawning (B. Morton, pers. comm. 1978).

Apart from the fact that it can recess into the sea bed (B. Morton, pers. comm., 1978) little is known of the reclining position of *Amusium*. Further information relevant to *P. (P.) laeviradiatum* may be gained through a comparison with the 'window pane oyster' *Placuna placenta* which at least in the form of the disc resembles *P. (P.) laeviradiatum*. *Pl. placenta* reclines at a slight angle to the sea bed with the dorsal third of the shell covered by sediment (Hornell, 1909). This apparently serves to stabilise the shell against current action and a similar reclining position can perhaps be envisaged for *P. (P.) laeviradiatum* with the dorsally extended auricles obviating any need for burial of the disc itself.

The usual occurrence of *P. (P.) laeviradiatum* in moderate numbers with a high diversity fauna suggests that it was an equilibrium species (Levinton, 1970).

9. FUNCTIONAL MORPHOLOGY

The following features of the disc are paradigmatic for a bivalve reclining in a high energy environment:

1. Large size
2. Thick shell
3. Strongly ornamented right valve
4. Smooth left valve
5. Low convexity

Of these, *P. (P.) laeviradiatum* exhibits only feature 5. The ornamentation of the right and left valves is exactly opposite to that of the paradigm. The fairly small adult size and thin shell is much closer to a paradigm for reclining on soft sediment in a low energy environment. Since there is abundant evidence (see Section 8) to show that *P. (P.) laeviradiatum* in fact occupied high energy environments it can be said that the species was poorly adapted to such situations. However, features which are inadaptive (small size, thin shell, reduced ornamentation) or of neutral significance (ontogenetic increase in UA) for reclining become adaptive for swimming. It seems probable therefore that *P. (P.) laeviradiatum* was able to recover from periodic overturning by means of the swimming response.

The small initial size and subsequent negative allometric growth of the byssal notch indicates only a brief byssate phase early in ontogeny. However, additional stability for the shell when adult may have been provided by burial of the elongate auricles just beneath the sediment surface, as suggested in Section 8. Most studied examples of slender, linear projections from the bulk of a shell (e. g. the alae of *Mucrospirifer* [Rudwick, 1970]) have been interpreted in terms of a 'snowshoe' adaptation to life on a soft substrate. From the evidence already adduced from ecology this cannot be the case for *P. (P.) laeviradiatum*. A more effective mode of stabilisation such as the spines of *Ps. (Ec.) barbatus* was probably precluded by the presence of a prismatic outer shell layer in the right valve (herein presumed to exist by analogy with other asymetrically ornamented members of the Propeamussiidae). Waller (1972a) has demonstrated the difficulty of forming sharply projecting ornament based on a prismatic microstructure. This also explains the absence of plicae in *P. (P.) laeviradiatum*. The internal costae of the species are almost certainly a functional substitute (see Part II).

Staesche (1926) speculated that the dorsally prolonged auricles acted like the keel of a boat and provided stability during swimming. To have been effective this would have required the animal to swim with the plane of commissure vertical. Since no extant pectinid is known to adopt this orientation Staesche's hypothesis must be classed as doubtful.

10. ORIGINS AND EVOLUTION

Of known species the only likely ancestor for *P. (P.) laeviradiatum* is *P. (P.) pumilum*. The lower density of external costae could be the result of heterochronic retardation (caused by changes in the regulatory genome) of the rate of costal intercalation in the latter species. The extended auricles of *P. (P.) laeviradiatum* cannot be the result of heterochronic alteration of the ontogeny of *P. (P.) pumilum* since the growth of the auricles in the latter species seems to be isometric. The development of extended auricles may therefore signify structural genome evolution. The smaller number of internal costae could represent nothing more than selection for the lower end of the range (9–13) in *P. (P.) pumilum*.

If *P. (P.) laeviradiatum* did indeed evolve from *P. (P.) pumilum* we witness the evolution of a strongly 'K' selected (stenotopic, equilibrium, moderate-sized) from a strongly 'r' selected (eurytopic, opportunistic, usually small-sized) species.

There is no evidence for any phyletic trends in morphology within *P. (P.) laeviradiatum* apart from a reduction in maximum height from the lowermost Aalenian (H_{max}: 30) to the L. Bajocian (H_{max}: 22.5).

If *P. (P.) laeviradiatum* became extinct after the Laeviuscula zone (see Section 5) no explanation can be put forward for its demise in terms of a loss of the appropriate sedimentary facies. Apparently suitable condensed deposits occur widely in the U. Bajocian of Europe.

Propeamussium (Propeamussium) nonarium
(Quenstedt 1858)

Pl. 1, Figs. 13, 14, ? Figs. 15, 16; text fig. 18

Synonymy

v* ? 1855	*Pecten lorierianus* sp. nov; Cotteau, p. 113.
1858	*Pecten nonarius* sp. nov; Quenstedt, p. 795, pl. 98, fig. 4.
? 1871	*Pecten penninicus* sp. nov; Neumayr, p. 375, pl. 21, fig. 4.
? 1874	*Pecten poecilographus* sp. nov; Gemmellaro and Di Blasi, p. 130, pl. 4, figs. 13–16.
pv non 1883	*Pecten poecilographus* Gemmellaro and Di Blasi; Boehm, p. 600, pl. 67, figs. 5, 6.
? 1893	*Pecten (Amusium) Sokolowi* sp. nov; Retowski, p. 284, pl. 14, figs. 24–26.
? 1893	*Pecten (Amusium) Pawlowi* sp. nov; Retowski, p. 285, pl. 14, figs. 27a, 27b.
1897	*Pecten Spendiarowi* sp. nov; Abel, p. 352, text figs. 1a, 1b.
1905	*Pecten Spendiarowi* Abel; Vetters, p. 250.
pv? 1905	*Pecten lorierianus* Cotteau; Peron, p. 234, pl. 10, figs. 8, 9.
non 1917	*Pecten Sokolowi* sp. nov; Borissiak and Ivanoff, p. 46, pl. 2, figs. 10, 10a.
v 1926	*Variamussium nonarium* (Quenstedt); Staesche, p. 88, pl. 3, figs. 9, 10.
? 1926	*Variamussium quinquenarium* sp. nov; Berckhemer in Staesche, p. 89, pl. 3, figs. 5, 6.
1964	*Variamussium nonarium* (Quenstedt); Wellnhofer, p. 37, pl. 2, figs. 4–7.
1974	*Propeamussium (Propeamussium) nonarium* (Quenstedt); Nitzopoulos, p. 46.
? 1978	*Parvamussium* aff. *personatum* (Goldfuss); Holder, p. 20, pl. 5, figs. 1–4, text fig. 11.

No trace of the type material of *Pecten nonarius* Quenstedt 1858, p. 795, pl. 98, fig. 4 has yet been found in the Quenstedt Collection (GPIT). The figured specimen was derived from the Malm ζ (L./M. Tithonian) of Söslingen (Swabia).

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

‚Nur den kleinen *Pecten nonarius* tab. 98, fig. 4 möchte ich besonders hervorheben, wie *undenarius* pag. 321 und Consorten zeigen die Steinkerne neun innere sehr dicke Hauptrippen. Bei großen, wie unsere Figur, stellt sich an Rande noch eine kurze Zwischenrippe ein. Im uebrigen läßt sich nicht viel wahrnehmen, man sieht nur, daß die Schale Ohren und feine Streifen hatte. Söslingen, Mähringen.'

2. AMENDED DIAGNOSIS

Distinguished from all other Jurassic species of *P. (Propeamussium)* by the intercalation of additional internal costae and by the termination of the internal costae somewhat farther from the ventral margin (at approx. 5/6 H).

3. AMENDED DESCRIPTION

Essentially similar to *P. (P.) pumilum;* differing by the smaller size (H rarely more than 8 mm) and by the ornament. Interior of valves ornamented with between 7 and 9 original radial costae, supplemented by intercalary costae at larger sizes but in neither case reaching the ventral margin (Pl. 1, Fig. 14). Exterior of left valve ornamented by more numerous original and intercalary costae, reaching the ventral margin and crossed by comarginal striae to form a reticulate pattern (Pl. 1, Fig. 13). Right valve exterior ornamented with comarginal striae.

4. DISCUSSION

'Pecten' lorierianus Cotteau may constitute the first name applied to the species described in Section 3. However, while the syntypes (MNS B. 03985; Pl. 1, Figs. 15, 16) apparently reveal traces of internal costae, of which some seem to be intercalary, there are only 5 or 6 original internal costae and some of the costae appear to reach the ventral margin. It seems unwise therefore to adopt *'P.' lorierianus* as the senior synonym. The next available name is *'P.' nonarius* Quenstedt. Although the type material has not yet been found the original description and figure leave no doubt as to its identity.

Abel's (1897) incomplete description of *'P.' Spendiarowi* mentions intercalary internal costae but also specifies external costae on the right valve, unlike *P. (P.) nonarium*. Vetters (1905) re-examined Abel's topotype material and showed the original description and figures to be composites built up from a number of poorly preserved specimens. Unfortunately, he did little to clarify the nature of the ornament on the right valve exterior. However, in other respects the revised description matches that of *P. (P.) nonarium* and it may well be that the uncertainty over the right valve exterior ornament is due to preservation of Abel's and Vetter's material as composite moulds, a common occurrence in thin shelled species.

One of the figures of *'P.' penninicus* Neumayr from the Oxfordian has the characteristic reticulate exterior ornament of *P. (P.) nonarium*, described by Staesche (1926). Neumayr referred this to the right valve in his diagnosis and considered that the other figure, characterised solely by comarginal ornament, represented the left valve. Hölder (1978) has re-examined Neumayr's types in Vienna and suggested that both may in fact be left valves which have been subjected to differing amounts of abrasion. There is thus no reason to exclude *'P.' penninicus* from *P. (P.) nonarium* on the basis of the external ornament. Unfortunately the types are not large enough to exhibit the diagnostic intercalary internal costae so the possibility cannot be entirely excluded that they are very late representatives of the externally similar species *P. (P.) pumilum;* they apparently possess 11 original internal costae as is common in the latter. Hölder has figured a similar specimen from the same horizon under *Parvamussium* aff. *personatum* (Goldfuss), a junior synonym of *P. (P.) pumilum*.

'P.' poecilographus Gemmellaro and Di Blasi may be a large form of *P. (P.) nonarium* (H: 44). The figured specimens are apparently steinkerns showing 10–12 original internal costae, with additional costae intercalated near the ventral margin. However, the disparity in size of the auricles (AH: 11, PH: 5.5 at H: 44) probably serves to distinguish the species. The internal ornament recognisable on specimens referred to *'P.' poecilographus* by Boehm (1883) is too faint for them to be regarded as conspecific with *P. (P.) nonarium*.

'Variamussium' quinquenarium Berckhemer is only known from two poorly preserved steinkerns (H_{max}: 28.6) showing 5–6 original internal costae with 2–3 intercalary costae between each pair. Their overall shape is similar to *P. (P.) nonarium* and they may therefore merely be large forms of this species.

'P.' ('Amusium') Pawlowi Retowski is only known from one imperfect specimen. The figure of this reveals 22 internal costae of which about 10 seem to be of intercalary origin. It is therefore very similar to *P. (P.) nonarium*. *'P.' ('Amusium') Sokolowi* Retowski was described as possessing 13–15 internal costal of which none were said to be intercalary. However, one of the original figures (pl. 14, fig. 26) is of a specimen with only 11 internal costae thus the species must be at least close to *P. (P.) nonarium*. *'P.' Sokolowi* Borissiak and Ivanoff (erected for a specimen referable to *Radulopecten fibrosus)* is a junior primary homonym of *'P.' ('Am.') Sokolowi* Retowski and must therefore be rejected.

5. STRATIGRAPHIC RANGE

P. (P.) nonarium is first recorded in the (?U) Oxfordian of S. Germany (Staesche, 1926; Nitzopoulos, 1974; ?Hölder, 1978) and ?S. Poland (Neumayr, 1871). Staesche also records the species in the Kimmeridgian of S. Germany and there are questionable records from the E. Paris Basin (see Section 7). Tithonian records are widespread and refer to numerous specimens although there are no certain records from the U. Tithonian. *'Parvamussium' hinagense* Tamura (1973) described from Japan and Indonesia may represent the persistence of *P. (P.) nonarium* into the L. Cretaceous.

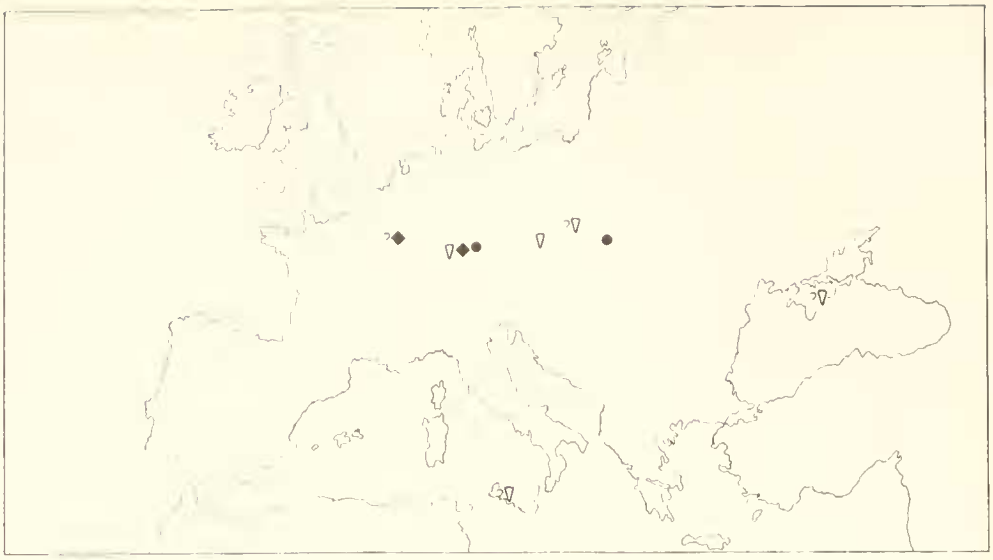
6. GEOGRAPHIC RANGE

P. (P.) nonarium is unknown outside the European region, except possibly in the L. Cretaceous (see Section 5). Within Europe (text. fig. 18) all records are limited to a narrow zone corresponding to a palaeolatitude of about 25°N. Occurrences outside this zone are of questionable identity (see Section 4).

7. DESCRIPTION OF ECOLOGY

Undoubted records of *P. (P.) nonarium* are limited to micritic or marly limestones containing a benthic fauna which is usually low in diversity and density. The only exceptions to this rule are specimens from reef-derived faunas in the Tithonian of Sicily which have been referred to *'Pecten' poecilographus* Gemmellaro and Di Blasi. This can be construed as further evidence for the view that the latter is not conspecific with *P. (P.) nonarium* (see Section 4).

In marly limestones of the L. Tithonian klippes north of Vienna *P. (P.) nonarium* occurs commonly in an otherwise sparse fauna dominated by ammonites but also containing a few terebratulid brachiopods and bivalves of the genera *Astarte*, *'Aucella'*, *Corbis*, *Nucula*, *'Ostrea'* and *Trigonia* (Abel, 1897; Vetters, 1905). Micritic limestones of the same age in S. Germany (Hangende Bankkalke) contain common *P. (P.) nonarium* associated with a similar low diversity benthos. In the M. Tithonian of the same area, the Neuburger



Text fig. 18: *Propeamussium (P.) nonarium* – European distribution.

Bankkalke, a micritic limestone, contains common *P. (P.) nonarium* in association with ammonites and small specimens of *Entolium* (Wellnhoffer, 1964).

Abundant but poorly preserved specimens exhibiting fine radial striae from the Calcaire à Astartes (L. Kimmeridgian) of the E. Paris Basin (MNR) are probably mainly referable to *Radulopecten strictus* (q. v.) but may also include a few examples of *P. (P.) nonarium*. Specimens with the diagnostic intercalary internal costae have, however, yet to be discovered.

8. INTERPRETATION OF ECOLOGY

The fine-grained sediments to which *P. (P.) nonarium* is limited are indicative of very low environmental energy. The sparseness of benthic fauna in such sediments suggests that they formed an unfavourable soupy substrate. *Entolium*, the only common epibenthic element apart from *P. (P.) nonarium*, probably escaped sinking into the substrate by virtue of the snowshoe effect provided by the small, thin, discoidal shell and by its probably considerable ability to swim. Non-vagile byssate and cemented bivalves were probably also restricted by the paucity of firm attachment sites. It is worth noting that the specimens of '*Ostrea*' are always found cemented to ammonites (Vetters, 1905).

P. (P.) nonarium may have been limited to low energy environments on account of its thin and probably weak shell. However, the very restricted geographic distribution of the species cannot be explained simply on this basis. Apparently suitable fine-grained substrates in, for instance, the U. Jurassic of S. Europe, went uncolonised. Bearing in mind the very narrow latitudinal range of *P. (P.) nonarium* it is possible that the species had a very precise temperature dependence.

9. FUNCTIONAL MORPHOLOGY

Small size, low convexity, discoidal form and thin shell place *P. (P.) nonarium* close to a paradigm for reclining on soft substrates in a low energy environment. The small byssal notch indicates only a brief byssate phase in the juvenile. The absence of information on the ontogeny of umbonal angle precludes any assessment of swimming ability although the above features are certainly not inadaptive for swimming. Internal costation probably provided strength and stiffness for the thin shell in defence against predatory attacks. Intercalation of new costae would have maintained this function against the detrimental effects of increased size and so represents a superior adaptation in comparison to the simple pattern of costae exhibited by other Jurassic species of *Propeamussium*.

10. ORIGINS AND EVOLUTION

By its general morphological similarity the most likely ancestor for *P. (P.) nonarium* is *P. (P.) pumilum*. However, there is an unexplained stratigraphic gap in the Callovian between respectively, the first and last appearances of these species.

At comparable sizes *P. (P.) nonarium* appears to have relatively fewer costae on the exterior of the left valve than *P. (P.) pumilum*. Since the costae are continuously intercalated during the ontogeny of both species, trans-specific evolution may have involved the heterochronic retardation of the rate of intercalation with respect to size. In contrast, the presence of internal intercalary costae in *P. (P.) nonarium* represents the evolution of a new feature and implies some more profound revolution in the genome. It represents, moreover, an improvement in mechanical design (see Section 9) and this, together with a narrowing in the range of substrate tolerance and retardation of 'shape' development, is strong evidence for the prevalence of 'K' selection (Gould, 1977).

From the limited available data it is impossible to detect any phyletic trends within *P. (P.) nonarium*.

Family PECTINIDAE Rafinesque 1815
Genus *ENTOLIUM* Meek 1865

Type species. OD; Meek 1865 p. 478; *Pecten demissus* Phillips, "as illustrated by Quenstedt, 1858, p. 353, pl. 48, fig. 7", i. e. *Entolium demissum* Meek 1865 (see Duff, 1978); Aalenian, Germany.

AMENDED DIAGNOSIS

Byssal notch usually absent at all stages of development; margins closed laterally; incised ligamental area usually present and extending parallel to hinge line on each side of inner ligament pit; auricular crura present; outer shell layer partly 'fibrous', 'fibres' radial or divaricate. M. Tr.-U. Cret., cosmop.

DISCUSSION

Hertlein (1969: N346) considered a byssal notch to be lacking in *Entolium*. There is, however, a small but quite clearly developed notch in juveniles of *Entolium (E.) lunare* (see p. 38). By his statement 'inner shell layer calcite, foliate; outer layer radially fibrous' Hertlein implies in his diagnosis the existence of only 2 shell layers in *Entolium*. However, in almost all known scallops, including the morphologically very similar *Amusium* (Taylor et al., 1969), there is a third non-myostracal shell layer, composed of aragonite. In all but the aberrant Propeamussiidae (see p. 22) this forms the middle shell layer and a similar layer can de inferred in *Entolium* (see p. 36). The inner and outer shell layers of Recent pectinids (sensu stricto) appear to be invariably composed of foliated calcite (Taylor et al., 1969). However, Hertlein's contention that Mesozoic *Entolium* has a fibrous outer layer is given support by the author's study of valve surfaces at low magnification (text fig. 27) although it would appear from specimens in various states of abrasion that only one sub-layer within the outer shell layer is composed of fibres. Indeed it is conceivable that the fibrous appearance could be due to the assumption of a vertical orientation by foliae. SEM study of fractured surfaces has not proved definitive on this point but henceforth in this work shell structures such as that depicted in text fig. 27 are termed fibrous in order to distinguish them from the more usual foliated structure consisting of sub-horizontal foliae. The mineralogy of the outer shell layer in *Entolium* is unclear from Hertlein's statement but the preservation state of specimens examined by the author suggests very strongly that it is calcitic, as is usual in the pectinids (see above).

Hertlein's statement that the fibres are radial must be amended on the basis of results presented herein so as to include divaricate arrangements. Such arrangements are also found in L. Jurassic *Camptonectes (C.) subulatus* (q. v.) thus forms of the latter with shallow byssal notches closely resemble contemporaneous *Entolium* (see p. 38). They may, however, be distinguished in well preserved specimens by the presence of divaricate *striae* on the shell surface (as against divaricate *fibres* within the shell of *Entolium*), by the absence of dorsally extended auricles on the right valve, by the perpendicular junction of the anterior auricle with the hinge line on the left valve and by the marked auricular asymmetry in both valves.

Subgenus *ENTOLIUM* s. s.

(Synonyms etc. *Protamusium* Verrill 1897
Protamussium Paris and Richardson 1916 [nom. null.]
Protomusium Stewart 1930 [nom. null.]
Entholium Tzankov and Boncev 1932 [nom. null.]
Etolium McLearn 1949 [nom. null.])

AMENDED DIAGNOSIS

Auricles of right valve projecting above hinge, commonly as angular wings; left valve smooth, right valve smooth or with comarginal grooves. M. Trias. – U. Cret., cosmop.

DISCUSSION

Hertlein (1969: N347) considered the valve bearing dorsally extended auricles in *E. (Entolium)* to be the left. However, the fact that in *E. (E.) lunare* (see p. 38) a byssal notch is found in the valve bearing dorsally extended auricles indicates, by analogy with all other known pectinids, that this valve is the right. Hertlein thought that the outer surface of the valves was always smooth in *E. (Entolium)*. The right valve of *E. (E.) orbiculare* (see p. 57) exhibits, however, quite strong comarginal grooves.

Staesche (1926) attempted to subdivide the bulk of Jurassic *E. (Entolium)* by the criterion of the presence or absence of internal ridges extending from the umbonal region in a direction sub-parallel to the dorsal margins. Forms with such ridges were said to posses umbonal angles of about 95° and were referred to the 'Gruppe des *Entolium cingulatum*' while forms without internal ridges were said to possess larger umbonal angles and were referred to the 'Gruppe des *Entolium demissum*'. Many subsequent authors have adopted Staesche's criteria yet they almost certainly represent a spurious basis for the subdivision of the majority of Jurassic *E. (Entolium)*. Staesche himself figured (pl. 4, fig. 5) a specimen of the exemplary species of his second group which shows, through the translucent shell, the internal ridges diagnostic of his first group. Moreover, the sole known type of this species (YM 202) has an umbonal angle of barely 80°. In fact umbonal angle increases through the ontogeny of virtually all Jurassic *E. (Entolium)* from a value below 95° to a value well above it, thus a single value cannot be diagnostic of any subdivision of the group. Furthermore internal ridges may be found in large specimens with correspondingly large umbonal angles as well as in small specimens with umbonal angles of about 95°. The author considers that in most cases the development of internal ridges, far from being under genetic control, is a result of diagenetic processes.

As Staesche pointed out, the internal ridges correspond in position to the margins of the relatively thick inner shell layer (composed of foliated calcite). In all known true pectinids (see above) this layer is surrounded in the internal surface by the outcrop of the middle shell layer and pallial myostracum, both of which are thin and composed of relatively soluble aragonite. In very many of those specimens of *E. (Entolium)* exhibiting internal ridges the upstanding feature appears to be nothing more than the edge of the inner shell layer, exaggerated by the loss of the immediately adjacent shell material. This is most plausibly explained as the result of the preferential dissolution of aragonite during diagenesis. Such a process could also account for the fact that in some specimens the external surface of the shell displays ridges above the edges of the inner shell layer (Pl. 1, Fig. 17). Although dissolution of aragonite would result in thinning of the shell in all but the most marginal regions (whose thickness is entirely due to the outer shell layer which is almost certainly composed of calcite, see p. 35) the proportionate effect on thickness would be greatest in the region immediately marginal to the inner shell layer where the middle shell layer and pallial myostracum constitute a relatively large part of the total thickness. Thus, in shells affected by diagenetic loss of aragonite, one might expect this region to be the locus of most compressive deformation due to sediment compaction with the resultant development of a ridge above the edges of the inner shell layer in a manner analogous to the genesis of a fault scarp.

In the case of certain specimens (BSPHG 1957 VI 1291–1293, 1824–1855) referred by Wellnhofer (1964) to *Entolium cingulatum* (Goldfuss) it does appear that internal ridges were present when the animal was alive. The grooves seen on internal moulds (cf. Pl. 1, Fig. 21) seem too sharply defined to have resulted from any diagenetic process of the sort outlined above. The author prefers at present to reserve judgement on the status of these specimens pending examination of further material (see also p. 52).

For the remainder of Jurassic *E. (Entolium)*, to which Staesche's scheme seems inapplicable, the only criteria by which a reasonable subdivision can be made are the presence or absence of a byssal notch and the presence or absence of strong comarginal grooves on the right valve. The first distinguishes between *E. (E.) lunare* and *E. (E.) corneolum* and the second between *E. (E.) orbiculare* and both the latter species. *E. (E.) orbiculare* and *E. (E.) corneolum* undoubtedley overlap in their stratigraphic ranges (see pp. 58, 52) and there is a strong suggestion that the latter species overlaps with *E. (E.) lunare* (see pp. 43, 52). There is thus no evidence that the species form part of a phyletic continuum. Kelly (1977) states that *E. (E.) orbiculare* may sometimes lack comarginal grooves on the right valve but that samples of *E. (Entolium)* can be assigned unequivocally to *E. (E.) orbiculare* if a few comarginally grooved right valves are present. This argument ignores the quite reasonable possibility that *E. (E.) orbiculare* may occur sympatrically with other *E. (Entolium)* species. Thus in the absence of any other diagnostic features in *E. (E.) orbiculare* the author can see no justification for not placing smooth right valves occurring together with comarginally grooved right valves in *E. (E.) corneolum* if (like all undoubted examples of *E. (E.) orbiculare* examined by the author) they lack a byssal notch or in *E. (E.) lunare* if (as Kelly states without pictorial evidence, may sometimes be the case in *E. (E.) orbiculare*) they possess a byssal notch. There is a pressing need for detailed study of undoubted (comarginally grooved) right valves of *E. (E.) orbiculare* in order to isolate further diagnostic features which could be used to cross-check Kelly's statements concerning the range of variation in the right valve.

At present there appears to be no completely sound basis for distinguishing the left valves of any of the three species discussed above. However, slight differences in mean metric proportions (see pp. 38, 47, 57) and the relatively limited overlap of the known stratigraphic ranges of the species (see pp. 43, 52, 58) do allow a reasonably confident identification of some specimens.

A further species which may be referable to *E. (Entolium)*, characterised by a slight byssal notch and very high HAA_R/L (see p. 43), appears to be quite common in the Tithonian of S. Europe. However like a number of other distinctive species from the latter stage and region (see p. 11) it is excluded from this work because of the paucity of museum specimens and bibliographic references and because its origins probably lie outside the pectinid fauna of the European Jurassic.

There is some evidence from the literature (see p. 58) for yet another *E. (Entolium)* species, characterised by strong comarginal ornament on both valves, in the M. Jurassic of Europe. However, the author has failed to discover any specimens which confirm the existence of this species.

The somewhat reduced mean H/UA of specimens with smooth, unnotched right valves from M. Tithonian sands near Oxford is not considered herein to merit a specific separation from *E. (E.) corneolum* since other metric proportions are inseparable from the latter species and a number of more parsimonious explanations, of which reduced growth rate is the most plausible (see p. 55), are available.

Entolium (Entolium) lunare (Roemer 1839)

Pl. 1, Figs. 17, 18, ? Fig. 23; text figs. 19–29.

Synonymy

? 1829	*Pecten* sp.; Phillips, pl. 5, fig. 11.
? 1833	*Pecten glaber* sp. nov; Hehl in v. Zieten, p. 69, pl. 53, fig. 1 (non Montagu sp.).
1836	*Pecten corneus* J. Sowerby, Goldfuss, p. 73, pl. 98, fig. 11 (non J. Sowerby sp.).
1839	*Pecten lunaris* sp. nov; Roemer, p. 26.
1843	*Pecten liasinus* sp. nov; Nyst, p. 299.
1850	*Pecten Hehlii* sp. nov; d'Orbigny, v. 1, p. 219.
v 1850	*Pecten disciformis* Schübler; d'Orbigny, v. 1, p. 237 (non Schübler sp.)
v? 1850	*Pecten Philenor* sp. nov; d'Orbigny, v. 1, p. 238.
v? 1850	*Pecten Palaemon* sp. nov; d'Orbigny, v. 1, p. 238, (Boule, 1908, v. 3, p. 37, pl. 18, fig. 5, non fig. 6).
v? 1850	*Pecten Proeteus* sp. nov; d'Orbigny, v. 1, p. 257.
(?) 1852	*Pecten glaber* Hehl; Quenstedt, p. 506 (non Montagu sp.).
1853	*Pecten glaber* δ var. nov; Oppel, p. 77 (non Montagu sp.).
? 1858	*Pecten amatus* sp. nov; Andler, p. 644.
(?) 1858	*Pecten glaber* Hehl; Quenstedt, p. 79 (non Montagu sp.).
? 1858	*Pecten sepultus* sp. nov; Quenstedt, p. 48, pl. 4, figs. 10, 11.
1858	*Pecten Hehli* d'Orbigny; Oppel, p. 103.
(?) 1858	*Pecten Philenor* d'Orbigny; Oppel, p. 181.
(?) *1861*	*Pecten sepultus* Quenstedt; Trautschold, p. 446.
1863	*Pecten liasinus* Nyst; Schlönbach, p. 545.
1864	*Pecten Hehli* d'Orbigny; Dumortier, p. 162, pl. 24, fig. 16.
? 1866	*Pecten demissus* Phillips; Lindstrom, p. 14, pl. 3, figs. 9, 10 (non Phillips sp.).

1867 *Pecten Hebli* D'Orbigny; Dumortier, p. 70, pl. 12, figs. 5, 6.
1868 *Pecten liasinus* Nyst; Jaubert, p. 234.
? 1869 *Pecten frontalis* sp. nov; Dumortier, p. 229, pl. 37, figs. 1, 2, pl. 38, fig. 1.
1869 *Pecten Palaemon* D'Orbigny; Dumortier, p. 304.
1869 *Pecten liasinus* Nyst; Dumortier, p. 306.
1871 *Pecten lunaris* Roemer; Brauns, p. 398.
1872 *Pecten liasinus* Nyst; Tietze, p. 106.
? 1875 *Pecten demissaries* sp. nov; Cross, p. 123.
1876 *Pecten lunularis* Roemer; Tate and Blake, p. 361.
v 1878 *Camptonectes liasicus* (Nyst); Bayle, pl. 121, fig. 2.
? 1883 *Pecten demissus* Phillips; Lundgren, p. 16, pl. 2, fig. 12 (non Phillips sp.).
1884 *Pecten lunularis* Roemer; Simpson, p. 172.
1886 *Pecten Hehli* D'Orbigny; Di Stefano, p. 135, pl. 4, figs. 28–30.
? 1886 *Pecten Di-Blasii* sp. nov; Di Stefano, p. 157, pl. 4, figs. 28, 29.
? 1888 *Pecten lundgreni* sp. nov; Moberg, p. 35, pl. 1, figs. 27–32.
1891 *Pecten Hehli* D'Orbigny; Behrendsen, p. 392.
? 1891 *Pecten Di Blasii* Di Stefano; Di Stefano, p. 61.
1892 *Pecten (Pseudamusium) Hehlii* D'Orbigny; Parona, p. 15.
(?) 1892 *Pecten (Pseudamusium) frontalis* Dumortier; Parona, p. 16.
1894 *Pecten Hehli* D'Orbigny; Möricke, p. 37.
? 1895 *Pecten Stewartianus* sp. nov; Lundgren, p. 198, pl. 3, fig. 12.
? 1895 *Pecten callosus* sp. nov; Lundgren, p. 200, pl. 3, fig. 15.
1897 *Pecten liasinus* Nyst; Pompeckj, pp. 773, 790, 820.
1903 *Pecten (Entolium) Hehli* D'Orbigny; Bistram, p. 38.
? 1904 *Chlamys (Pseudamussium) Chartroni* sp. nov; Cossmann, p. 504, pl. 16, figs. 11, 12.
1909 *Pecten (Entolium) Hehli* D'Orbigny; Trauth, p. 88.
1909 *Pecten (Entolium) liasinus* Nyst; Trauth, p. 89.
1912 *Pecten Hehli* D'Orbigny; Toni, p. 33.
1915 *Pecten (Entolium) Fraiponti* sp. nov; Rollier, p. 467, pl. 30, fig. 7.
non 1916 *Chlamys (Pseudamussium) palaemon* (D'Orbigny); Cossmann, p. 46, pl. 5, figs. 18-20.
1916 *Entolium disciforme* (Schübler); Cossmann, p. 45, pl. 8, figs. 10, 11 (non Schübler sp.).
? 1916 *Pecten glaphyrus* sp. nov; R. Philippi in Jaworski, p. 437.
? 1917 *Pecten vitreus* Roemer; Borissiak and Ivanoff, p. 8, pl. 1, fig. 4, (non figs. 1, 2, 12, 16).
1925 *Pecten (Entolium) Hehli* D'Orbigny; Dubar, pp. 260, 266.
1925 *Pecten liasinus* Nyst; Dubar, p. 266.
(?) 1925 *Pecten frontalis* Dumortier; Dubar, p. 266.
(?) 1925 *Pecten (Pseudamussium) Palaemon* D'Orbigny; Dubar, p. 266.
v 1926 *Chlamys calva* (Goldfuss); Staesche, p. 58, pl. 2, figs. 11, 12, (non Goldfuss sp.).
v 1926 *Entolium Hehlii* (D'Orbigny); Staesche, p. 59, pl. 2, figs. 13–15.
v 1926 *Chlamys Philenor* (D'Orbigny); Staesche, p. 62, pl. 1, figs. 16, 17.
v? 1926 *Entolium Proeteus* (D'Orbigny); Staesche, p. 92, pl. 6, figs. 3, 4.
v 1926 *Entolium lunare* (Roemer); Staesche, p. 96, pl. 4, figs. 1, 2.
v 1926 *Entolium liasinum* (Nyst); Staesche, p. 97, pl. 6, fig. 5.
(?) *1926* *Entolium frontalis* (Dumortier); Roman, p. 113.
(?) *1929* *Pecten (Amussium) Palaemon* D'Orbigny; Lanquine, pp. 132, 189.
1929 *Pecten (Entolium) Hehli* D'Orbigny; Lanquine, p. 132.
1932 *Pecten (Entholium) liasinum* Nyst; Tzankov and Boncev, p. 230.
(?) 1934 *Entolium frontale* (Dumortier); Rosenkrantz, p. 113.
v 1936 *Entolium Hehlii* (D'Orbigny); Dechaseaux, p. 60, pl. 8, figs. 10, 11.
(?) 1936 *Entolium frontalis* (Dumortier); Dechaseaux, p. 62.
1936 *Entolium Fraiponti* (Rollier); Dechaseaux, p. 62.
v? 1936 *Chlamys philenor* (D'Orbigny); Kühn, p. 247, pl. 12, fig. 29.
(?) 1942 *Pseudentolium frontale* (Dumortier); Rosenkrantz, p. 25.
1942 *Pecten (Entolium)* cf. *Hehli* D'Orbigny; Leanza, p. 175, pl. 9, fig. 4.
1951 *Entolium hehli* D'Orbigny; Troedsson, p. 216.
1951 *Entolium calvum* (Goldfuss); Troedsson, p. 217, pl. 20, figs. 9–13 (non Goldfuss sp.).
1951 *Entolium lundgreni* (Moberg); Troedsson, p. 218, pl. 20, figs. 4–8.
1961 *Entolium* cf. *lunare* (Roemer); Hayami, p. 255.
1963 *Entolium lunare* (Roemer); Hallam, p. 561.
(?) *1965* *Pecten frontalis* Dumortier; Dahm, pp. 27, 28.
1966 *Entolium proteus* (D'Orbigny); Behmel and Geyer, p. 28.
1966 *Entolium lunare* (Roemer); Urlichs, p. 31.
1966a *Entolium liasinum* (Nyst); C. Palmer, p. 67.
1966b *Entolium liasinum* (Nyst); C. Palmer, p. 72.
1967 *Entolium liasinum* (Nyst); Berridge and Ivimey Cook, p. 160.
1971 *Entolium liasinum* (Nyst); Hallam, pp. 244, 245.
? *1971* *Entolium proeteus* (D'Orbigny); Wendt, p. 156.
1973 *Entolium (Entolium) Hehli* (D'Orbigny); Lentini, p. 23, pl. 14, fig. 7.
? 1978 *Entolium* sp. A; Duff, p. 64, pl. 5, figs. 7–10, 12, 13, 17.

The type material (possibly only one specimen) of *Pecten lunaris* Roemer 1839, p. 26 is probably in the Roemer-Pelizaeus-Museum, Hildesheim, W. Germany. Roemer cites the following dimensions: 'Diameter': 3.5 inches (88 mm), UA: 150. The material was collected near Ocker (N. Germany), according to Brauns (1871) from sediments of the Planorbis zone.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

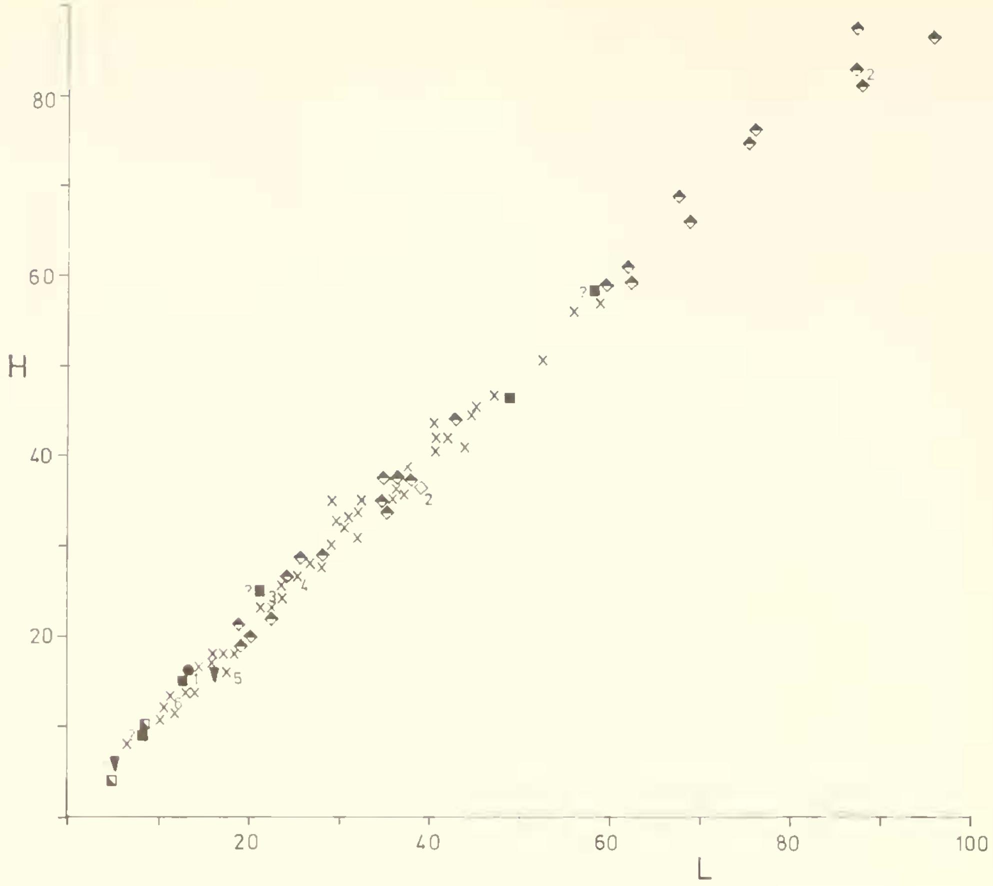
'*P. (Pleuronectes)* testa plana orbiculari concentrice substriata, angulo marginum cardinalium obtusissimo.

Es gehört diese Form zu den Pleuronectiden. Die Schalen sind sehr flach gewölbt, zirkelrund, nur undeutlich concentrisch gestreift und ziemlich dick. Die Schloßkantenwinkel beträgt etwa 150 Grad.

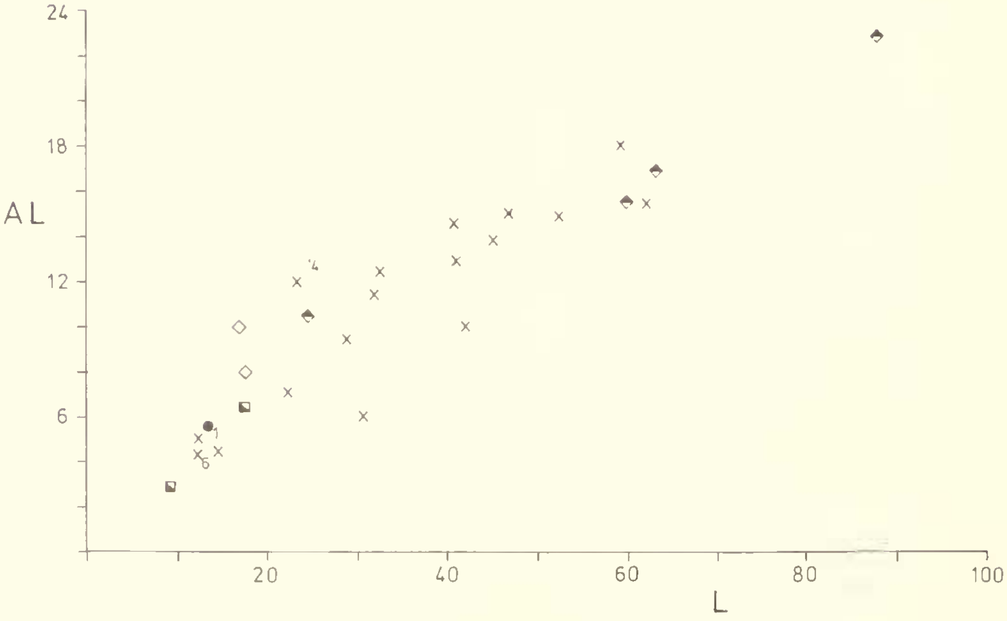
Findet sich im unteren Lias des Adenberges bei Ocker und hat einen Durchmesser von $3^{1}/_{2}$ Zoll.'

2. AMENDED DIAGNOSIS

Distinguished from *E. (E.) corneolum* by the presence of a small byssal notch in the juvenile and from *E. (E.) orbiculare* by the smooth right valve.



Text fig. 19: *Entolium (E.) lunare* – height/length.



Text fig. 20: *Entolium (E.) lunare* – separation of auricular apices/length.

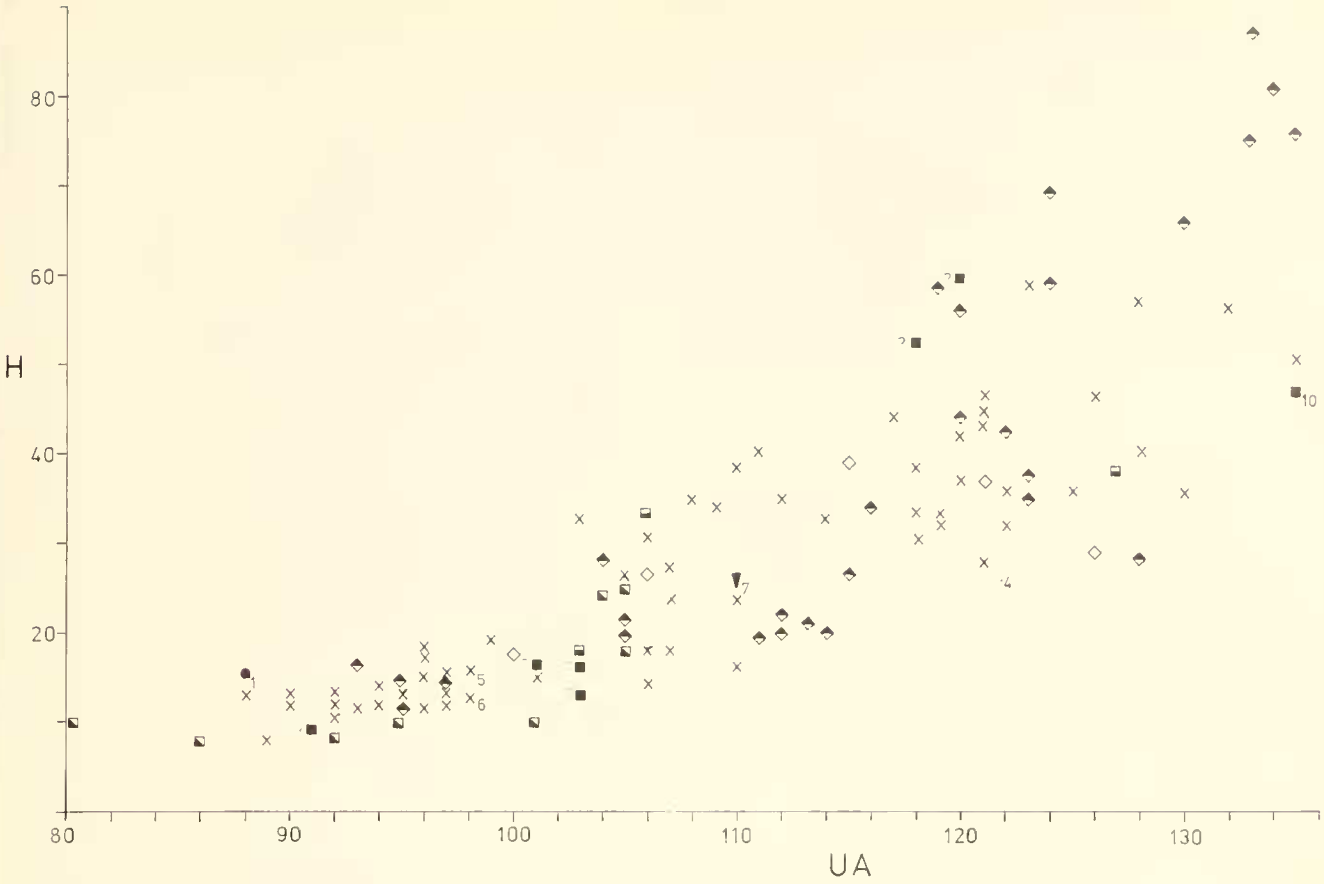
3. AMENDED DESCRIPTION

Disc sub-ovate, higher than long early in ontogeny, becoming longer than high (text fig. 19). Maximum height probably 116 mm (BM 46444) but possibly as much as 145 mm (see Section 4). Umbonal angle relatively invariant at any one size but increasing at a decreasing rate during ontogeny (text fig. 21) to give concave dorsal margins.

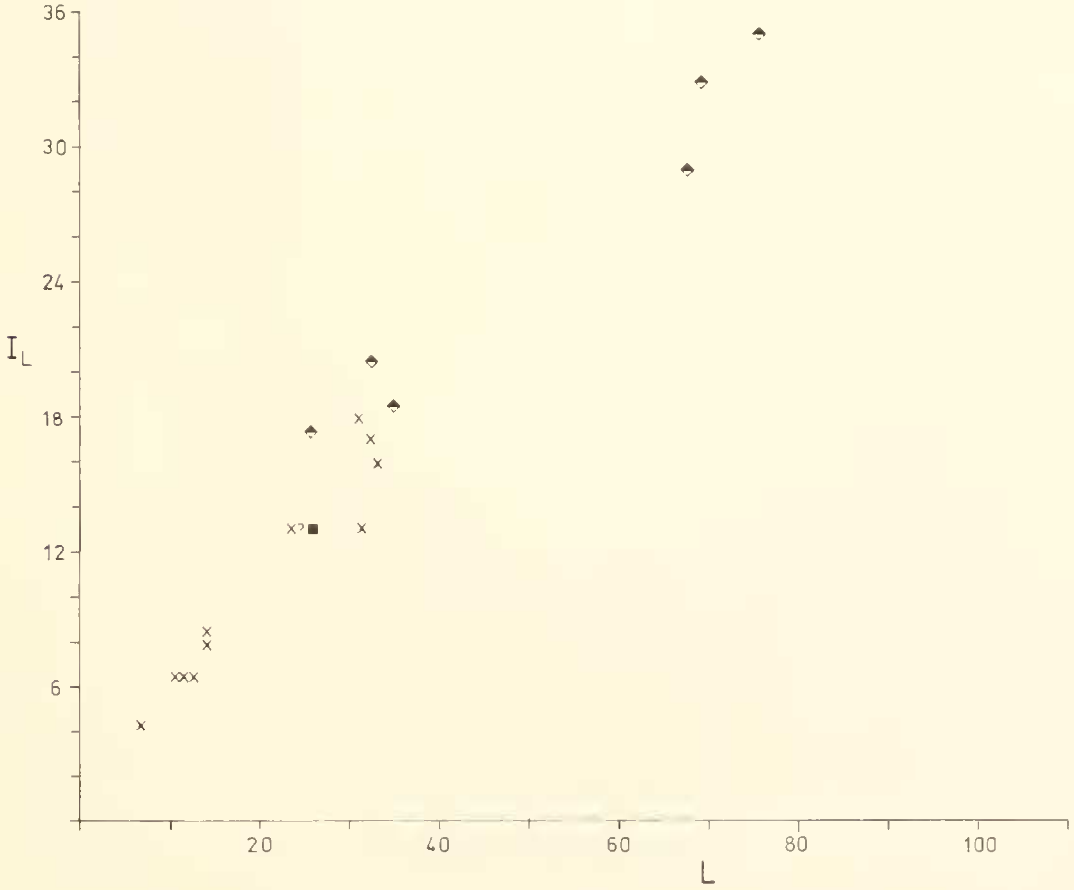
Equilateral, approximately equivalve, low convexity.

Intersinal distance slightly greater in left valve than right, increasing at a decreasing rate in both (text figs. 22, 23). Small juvenile byssal notch becoming almost non-existent later in ontogeny (Pl. 1, Fig. 18).

Disc flanks low but auricles well demarcated from disc. On left valve both auricles meeting hinge at an obtuse angle and



Text fig. 21: *Entolium (E.) lunare* – height/umbonal angle.



Text fig. 22: *Entolium (E.) lunare* – intersinal distance on left valve/length.

disc at an acute angle. On right valve both auricles extended dorsally beyond hinge line, posterior meeting disc at an acute angle, anterior meeting disc at an approximate right angle. Height of right valve anterior auricle (text fig. 24) and separation of auricular apices (text fig. 20) variable and increasing at a decreasing rate in both. Anterior hinge length slightly greater than posterior, increasing at a decreasing rate in both (text figs. 25, 26).

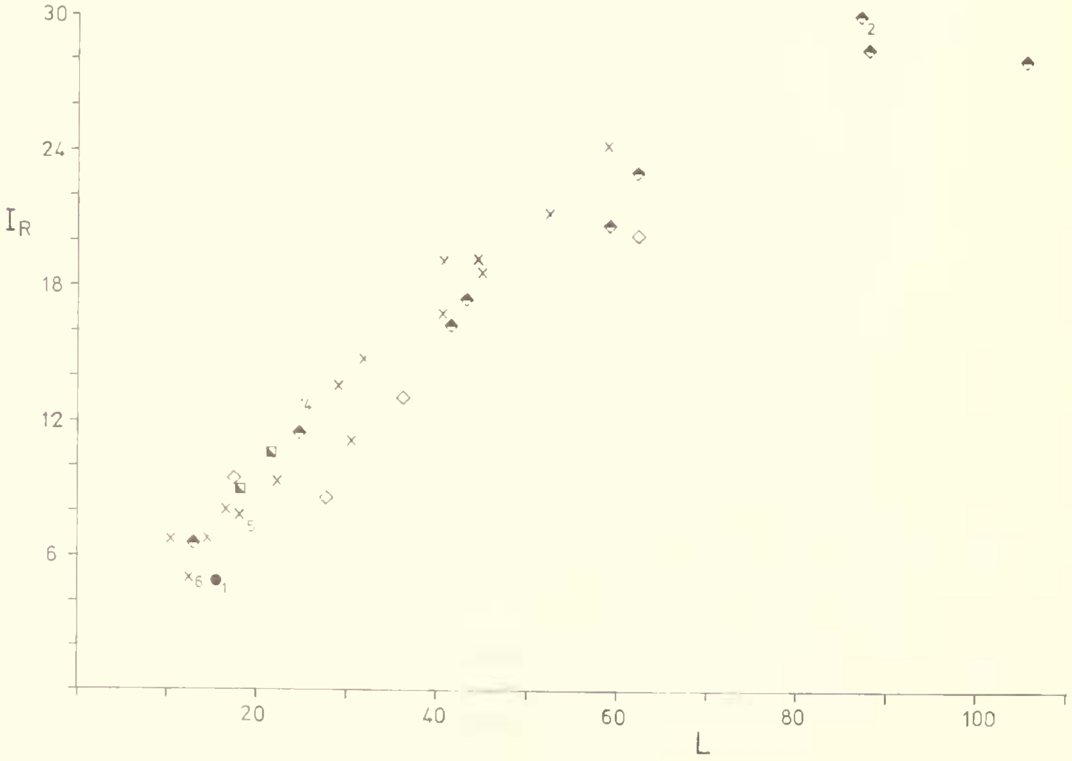
Valve exteriors ornamented only with very fine comarginal striae. Shell thin with at least one sub-layer in the outer shell layer composed of divaricate fibres (text fig. 27; see p. 35).

4. DISCUSSION

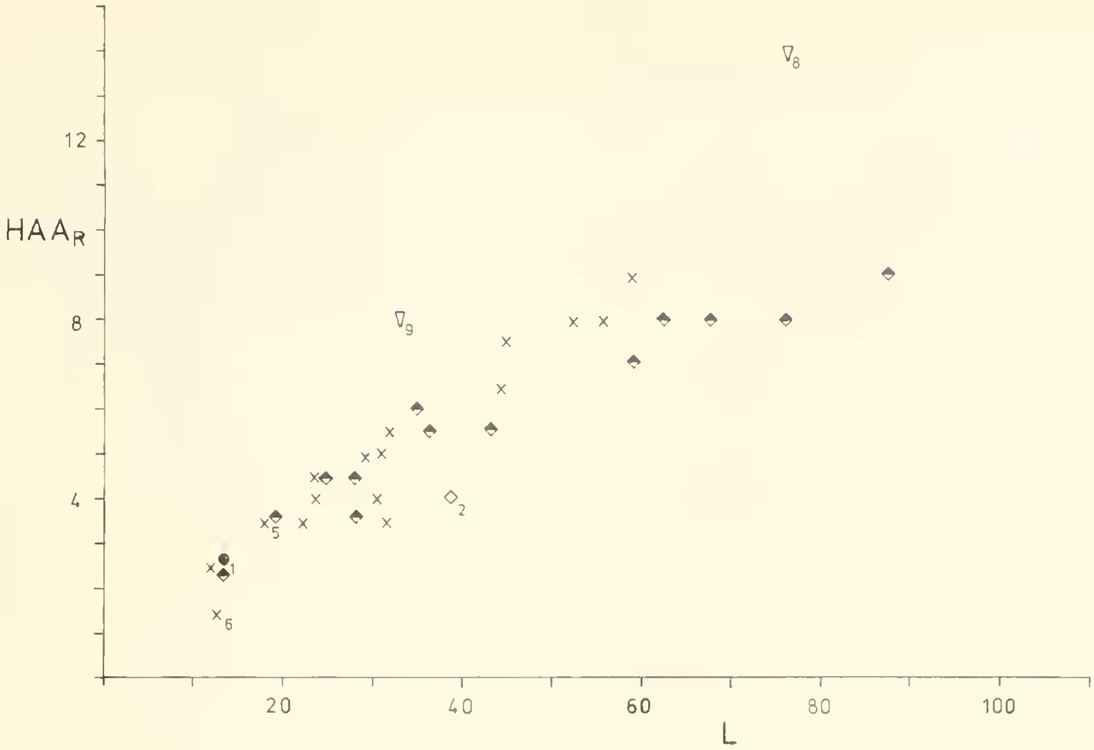
Possibly the earliest bibliographic record of the species described in Section 3 is as *'Pecten'* sp. Phillips (1). The stratigraphic horizon of the figured specimen is unusually late (Oxfordian) but the presence of a byssal notch aligns it with the species described above (however, see below). The original is now lost, as is that of *'P.' glaber* Hehl whose figure also resembles that of the species described in Section 3. In erecting *'P.' Hehlii* for Hehl's figured specimen, d'Orbigny (1850) considered that *'P.' glaber* was a junior primary homonym of a species described by Montagu in 1803. His hypodigm is far from clear but subsequent authors (see Synonymy) have applied the name to the species described in Section 3. The present author has been unable to trace Montagu's description but even assuming that d'Orbigny was justified in rejecting Hehl's species, the creation of a new species was an unnecessary step since both *'P.' lunaris* Roemer and *'P.' liasinus* Nyst appear to represent the species described in Section 3, and have historical precedence. *'P.' liasinus* was created in 1843 for Goldfuss' (1836) specimen from the L. Jurassic referred to *'P.' corneus* J. Sowerby, a Tertiary species. *'P.' lunaris* was erected in 1839 for a specimen which, according to Brauns (1871), was derived from the Planorbis zone. The specimen has not been examined by the present author. However, Roemer specifies an umbonal angle of 150° which is a reasonable value for the species described in Section 3 at the size stated ('diameter': 87 mm) and well above that attained in any other Jurassic *E. (Entolium)* species. Together with the stratigraphic information this can leave little doubt that *'P.' lunaris* should be accorded the status of senior synonym.

One of the syntypes of *'P.' Palaemon* d'Orbigny (MNS 1840) closely resembles *E. (E.) lunare* in its ornament and metric proportions (2). However, the other syntype is closer to *Chlamys (Ch.) textoria* in its possession of radial striae and since such ornament was specified in d'Orbigny's description, the latter specimen should perhaps be selected as lectotype. This interpretation appears to have been followed by Cossmann (1916) and Dumortier (1869).

'P.' Philenor d'Orbigny was created for L. Pliensbachian specimens which fell within Goldfuss' (1836) hypodigm for *'P.' cingulatus*, an *E. (Entolium)* species. In so far as there are apparently no European L. Pliensbachian *E. (Entolium)* species apart from *E. (E.) lunare*, d'Orbigny's hypodigm must be included in the latter species concept. However the single observed type (MNO 1843) is probably a representative of *Ch. (Ch.) textoria* so the status of secondary references to d'Orbigny's species for which no original remains (e. g. Oppel, 1858) is in some doubt. The figured originals of Staesche's (1926) *'Ch.' Philenor* (GPIT) are almost certainly representative of *E. (E.) lunare* but that of Kuhn's (1936) *'Ch.' philenor* (BSPHG) is more reminiscent of *Camptonectes (C.) subulatus.*



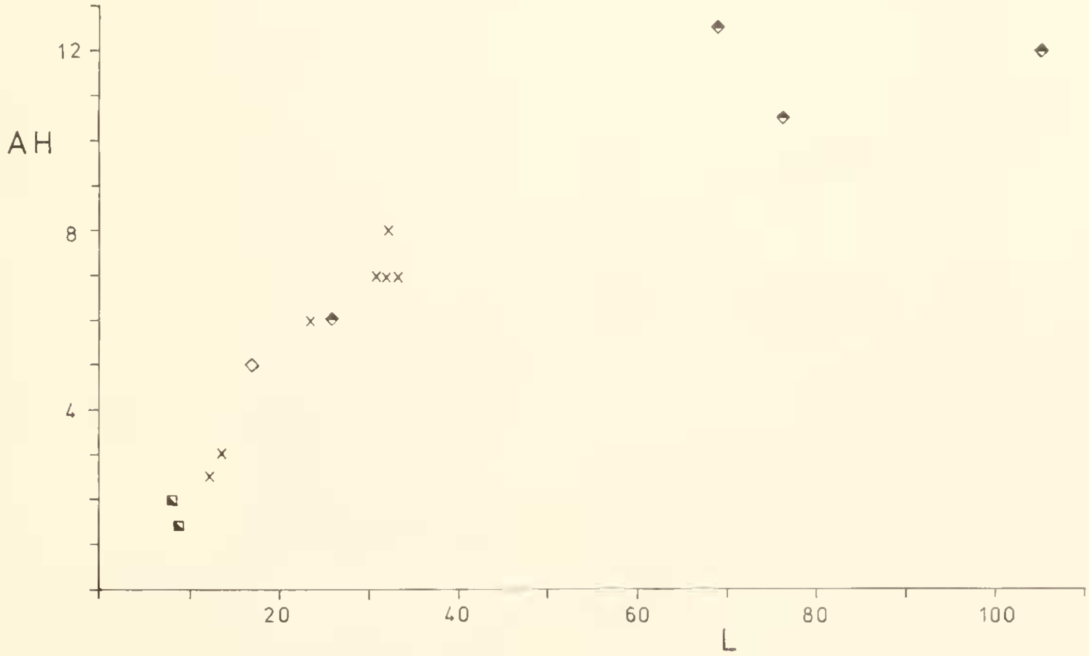
Text fig. 23: *Entolium (E.) lunare* – intersinal distance on right valve/length.



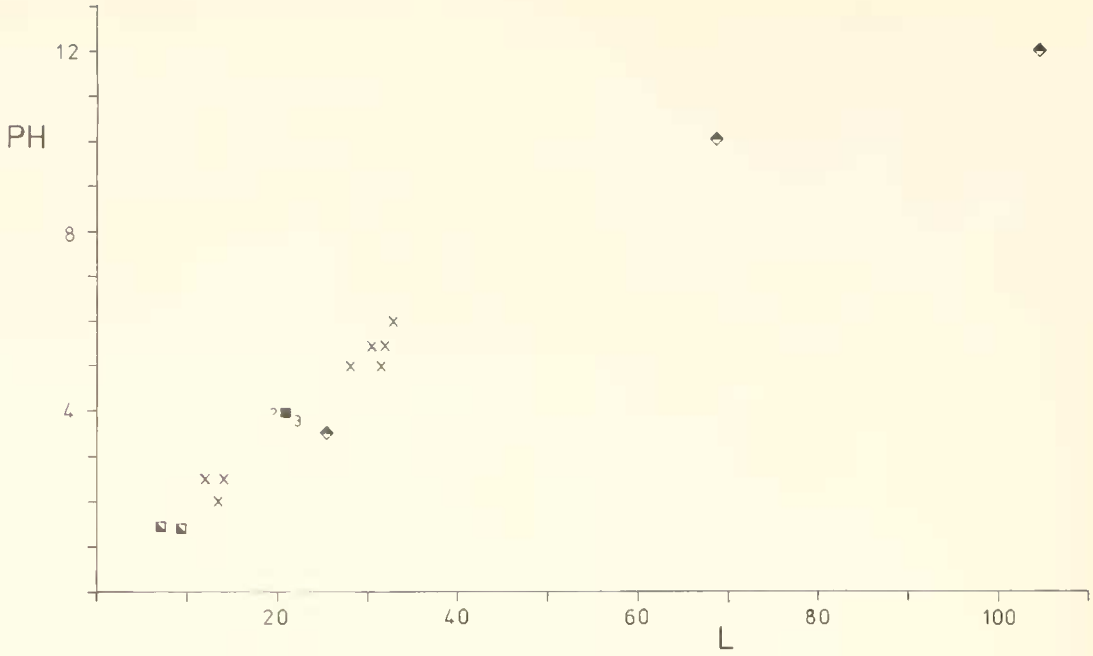
Text fig. 24: *Entolium (E.) lunare* – height of anterior auricle on right valve/length.

In the same way as for *'P.' Philenor*, d'Orbigny created *'P.' Proeteus* for Toarcian specimens which fell within Goldfuss' hypodigm for *'P.' cingulatus*. Since two *E. (Entolium)* species *(E. (E.) lunare* and *E. (E.) corneolum)* appear to coexist in the Toarcian it is impossible to be certain of d'Orbigny's hypodigm in the absence of a diagnosis. The only syntype which the author has been able to discover (MNO 2079) is too poorly preserved for specific determination although H/L and PH/L (3) plot within the range of *E. (E.) lunare*. Staesche's (1926) figured originals to *E. Proeteus* (GPIT) are similarly indeterminate and thus specimens referred to this species by the latter author in Behmel and Geyer (1966) are also of uncertain affinities. Wendt's (1971) record from the Aalenian and Bajocian of Sicily almost certainly refers to *E. (E.) corneolum*.

A specimen (MNS) from the L. Pliensbachian referred by d'Orbigny to Schübler's (1833) Bajocian species *'P.' disciformis* (= *E. (E.) corneolum* q. v.) in fact possesses the small auricles typical of *E. (E.) lunare*. Similarly, a specimen from the same horizon referred to Schübler's species by Cossmann (1916) has the small byssal notch of *E. (E.) lunare*. Bearing in mind the known stratigraphic range of *E. (E.) corneolum* it



Text fig. 25: *Entolium (E.) lunare* – anterior hinge length/length.



Text fig. 26: *Entolium (E.) lunare* – posterior hinge length/length.

seems highly likely that unillustrated reports of pre-Toarcian occurrences of Schübler's species (Coquand, 1860; Terquem and Piette, 1865; Pompeckj, 1897; Joly, 1907; Dubar, 1925; Lanquine, 1929; Dechaseaux, 1936) together with Leanza's (1942) and Lentini's (1973) poorly illustrated examples are in fact referable to *E. (E.) lunare*. Goldfuss' (1836) record of L. Jurassic examples of Phillips' species '*P.*' *demissus* is likewise almost certainly a misnomer for *E. (E.) lunare*; his figured specimen (BSPHG) is from the M. Jurassic. However, specimens figured under '*P.*' *demissus* from an unspecified horizon in Spitzbergen (Lindstrom, 1866; Lundgren, 1883) exhibit the byssal notch typical of *E. (E.) lunare* and thus, bearing in mind the very limited development of the L. Jurassic in Spitzbergen, may constitute M. or even U. Jurassic representatives of the latter species. '*P.*' *Stewartianus* Lundgren from an unspecified horizon in E. Greenland has a slight byssal notch and H/UA (150/140) within the range of *E. (E.) lunare* projected to larger sizes. It may be an U. Jurassic representative of the latter since it was compared with a species described from the Kimmeridgian, '*P.*' *validus* Lindstrom (= *Camptonectes (C.) auritus*).

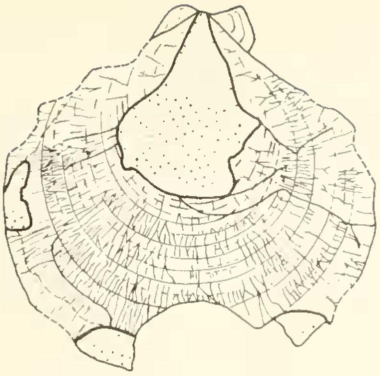
Borissiak and Ivanoff's (1917, pl. 1, fig. 4) figure of '*P.*' *vitreus* (non Roemer) depicts a specimen with a byssal notch that is undoubtedly from the L. Volgian (≃ L. Tithonian) of Russia. However, it should be borne in mind for this and the above records from Spitzbergen and Greenland that *E. (E.) orbiculare* (q. v.) is present in the U. Jurassic of each area and since Kelly (1977) states that the right valve of the latter species may be smooth and possess a byssal notch there remains the possibility that *E. (E.) orbiculare* may be the only species present (however see p. 36). There is a rather more remote possibility that the above records may refer to a poorly known, essentially S. European species (see below).

'*P.*' *callosus* Lundgren, from E. Greenland, has metric proportions (4) within the range of *E. (E.) lunare*.

The figures of '*P.*' *lundgreni* Moberg from S. W. Sweden appear to show divaricate striae and are thus indicative of *Camptonectes*. However, Troedsson (1951), who may have examined the types, has referred to Moberg's species specimens whose small byssal notch, H/L, H/UA, l_R/L and HAA_R/L (5) is within the range of *E. (E.) lunare*. Metric proportions of Moberg's figure (6) are also indistinguishable so the appearance of divaricate striae may be a misrepresentation of the divaricate fibres within the shell of *E. (E.) lunare*.

AH/L (46/130) and l_R/L (60.5/130) of the figure (1869, pl. 37, fig. 1) of '*P.*' *frontalis* Dumortier from the U. Pliensbachian are considerably higher than those of measured specimens of *E. (E.) lunare*. However, this may well be due to inaccurate representation of the original for which Dumortier cites a height of 145 mm and length of 155 mm. Subsequent references to Dumortier's species in Parona (1892), Roman (1926), Rosenkrantz (1934, 1942) and Dechaseaux (1936) are unaccompanied by figures so must remain doubtful. '*P.*' *(Entolium) Fraiponti* Rollier, which was thought to represent possibly no more than a geographic race of '*P.*' *frontalis* has H/UA (104/140) within the range of *E. (E.) lunare* projected to larger sizes. H/UA of the figure of '*Ch.*' ('*Pseudamussium*') *chartroni* Cossman (7) from the Hettangian of France is also within the range of *E. (E.) lunare*. The depth of the byssal notch is more reminiscent of *C. (C.) subulatus* but in spite of Cossmann's statement to the contrary the auricles of one figured specimen extend dorsally beyond the hinge line so his species may be an early and morphologically extreme representative of *E. (E.) lunare*. '*P.*' *Di-Blasii* Di Stefano, from the L. Lias of Sicily has rather pronounced comarginal ornament but as it is in other respects identical to *E. (E.) lunare* this may be another aspect of variation.

The equal-sized auricles of '*P.*' *sepultus* Quenstedt, a small smooth species from the L. Lias of Swabia, suggest that it belongs to *E. (E.) lunare* rather than the common co-occurring



Text fig. 27: Outer surface of a slightly abraded right valve of *Entolium (E.) lunare* showing divaricate fibres. Specimen (BSPHG 1983 XVII 8) from Frodingham Ironstone; × 1.6.

species *C. (C.) subulatus*. However, the affinities of *'P.' amatus* ANDLER, from the same horizon and region, diagnosed merely as a smooth flat shell with comarginal striae, could lie with either of the above species. *'P.' demissaries* CROSS was given a similarly inadequate diagnosis but is probably synonymous with *E. (E.) lunare* rather than *C. (C.) subulatus* since the horizon of derivation (Frodingham Ironstone) is one in which the former species is much more abundant than the latter (see Section 7).

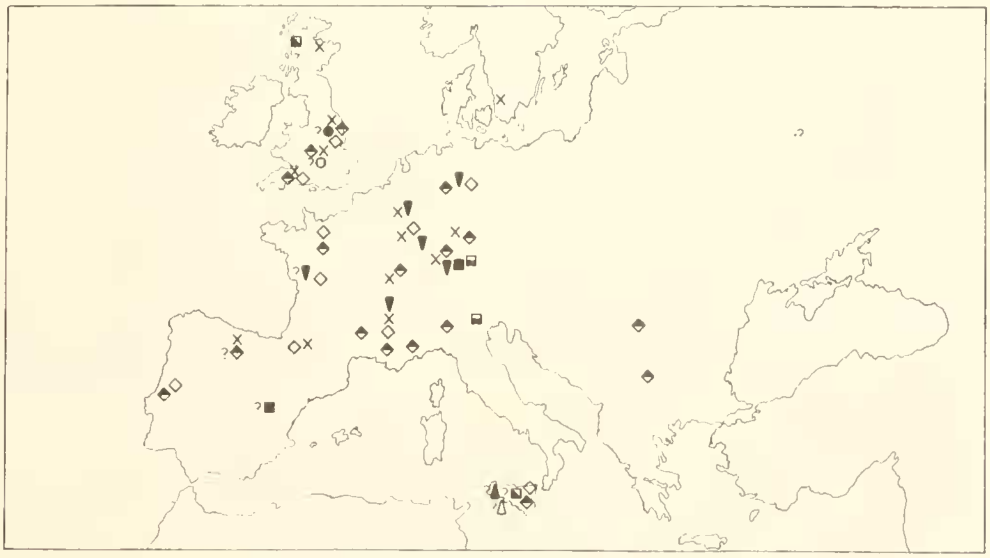
'P.' glaphyrus R. PHILIPPI was distinguished from the Callovian species *'P.' demissus* (= *E. (E.) corneolum*) by the relatively undiagnostic criterion of auricle angularity. However, in so far as the species is described from the U. Pliensbachian (prior to certain records of *E. (E.) corneolum*) it probably belongs to *E. (E.) lunare*. Although described from the Callovian *Entolium* sp. A. DUFF has a clear byssal notch, unlike the much more common contemporaneous species *E. (E.) corneolum*, and may therefore be a late representative of *E. (E.) lunare*. The small size of the available material does not however allow exclusion of the possibility that *E.* sp. A is an early representative of *E. (E.) orbiculare* (see above) or an essentially S. European Tithonian species which bears a superfical resemblance to *E. (E.) lunare* but which can be readily distinguished in large specimens by the much higher HAA_R/L (8, 9; specimens referred respectively to *'P.' insularum* D'ORBIGNY [MNS] and *'Ch.'* cf. *poecilographa* GEMMELLARO and DI BLASI [GPIT]).

GOLDFUSS' (1836) name *'P.' calvus* (= *C. (C.) subulatus* q. v.) has been misapplied by STAESCHE (1926) and TROEDSSON (1951) to figured specimens with the small byssal notch typical of *E. (E.) lunare*. It is thus possible that unillustrated records of GOLDFUSS' species in D'ORBIGNY (1850), TATE and BLAKE (1876) and JOLY (1907) may also refer to *E. (E.) lunare*.

5. STRATIGRAPHIC RANGE

Two specimens from the Planorbis zone (Hettangian) of the Italian Alps (BISTRAM, 1903) together with an indeterminate number of specimens from the same horizon in S. Germany (STAESCHE, 1926), ROEMER's (1839) material, probably from N. Germany, and questionable specimens from the W. Paris Basin (COSSMANN, 1904; see Section 4) constitute the earliest records of *E. (E.) lunare*. The species is recorded rarely in the Angulata zone of the Rhone basin (DUMORTIER, 1864) and may also occur at the same horizon in S. Germany (ANDLER, 1858; see Section 4). DECHASEAUX (1836) records the species from an unspecified horizon in the Hettangian of the E. Paris Basin. *E. (E.) lunare* becomes common in the Bucklandi zone and is thereafter widespread and locally common until the U. Pliensbachian. Toarcian records are equivocal because all potential examples of *E. (E.) lunare* have poorly preserved auricles and so cannot definitely be separated from *E. (E.) corneolum* by the diagnostic criterion. However, a specimen in the GPIG (Pl. 1, Fig. 23) from the Toarcian of S. Germany has H/UA (10) well outside the range of *E. (E.) corneolum* and this specimen together with four others from the same area in the GPIT, one from Yorkshire (SM J50642) and one from Gloucestershire (BM L94280), all of which plot within the range of text fig. 21, seems to indicate that *E. (E.) lunare* extended into the Toarcian. All but the first mentioned are from the upper substage.

M. and U. Jurassic bibliographic records which may refer to *E. (E.) lunare* must be treated with great caution (see Sec-



Text fig. 28: *Entolium (E.) lunare* – European distribution.

Text fig. 29: *Entolium (E.) lunare* – World distribution (Pliensbachian reconstruction).

tion 4). A slight byssal notch is present in a smooth right valve (OUM J26053) from the L. Tithonian (Pectinatus zone) near Oxford but in view of the possible development of such a morphology in *E. (E.) orbiculare* (see p. 36) it can only tentatively be accepted as an U. Jurassic record of *E. (E.) lunare*.

6. GEOGRAPHIC RANGE

Within Europe (text fig. 28) *E. (E.) lunare* is a widespread species. Outside Europe (text fig. 29) occurrences are widely dispersed and are not connected by obvious migration routes. Records from S. America might be understood as the result of a migration along the northern shores of Tethys by linking occurrences in the Carpathians (Pompeckj, 1897) and Japan (Hayami, 1961). However depending on the tectonic reconstruction adopted records from the Carpathians might be held to indicate migration along the southern shores of Tethys, perhaps utilising a marine connection between Africa, Antarctica and S. America (see p. 25).

7. DESCRIPTION OF ECOLOGY

E. (E.) lunare first occurs commonly in the Arietenkalk (L. Sinemurian, Bucklandi zone) of S. W. Germany in association with quite common examples of *Camptonectes (C.) subulatus* and *Chlamys (Ch.) textoria*. The maximum height of *E. (E.) lunare* is 51 mm (GPIT). Deposits of the same age and probably similar facies in the Rhone also contain abundant *E. (E.) lunare* in association with *Pseudopecten (Ps.) èquivalvis* (Dumortier, 1867). In the U. Sinemurian (Obtusum zone) part of the Frodingham Ironstone, a condensed chamosite oolite in Lincolnshire, *E. (E.) lunare* occurs with all the above species but is much the most numerous element of the fauna, attaining a maximum height of 57 mm (ScM 1099). In contemporaneous argillaceous facies (Hallam, 1963) and similar facies in the L. Pliensbachian *E. (E.) lunare* is greatly outnumbered by *C. (C.) subulatus*. However, in neretic limestones, probably of L. Pliensbachian age (see p. 79) in Sicily (Di Stefano, 1886) *C. (C.) subulatus* is absent and *E. (E.) lunare* occurs commonly with *Ps. (Ps.) veyrasensis*. L. Pliensbachian sandstones in E. Greenland (Rosenkrantz, 1934) are reported to contain abundant examples of *E. frontale* (Dumortier), a probable synonym of *E. (E.) lunare* (see Section 4) in association with common *Ps. (Ps.) equivalvis*. The latter species greatly outnumbers *E. (E.) lunare* in the condensed chamosite oolites (*'Pecten'* Beds) of the Ibex zone in Gloucestershire and Lincolnshire and in sandstones (Sandy Series) and condensed chamosite oolites (Cleveland Ironstone) of the Margaritatus zone in Yorkshire. A similar situation pertains in ironstones of the Spinatum zone (Marlstone) in the Midlands where the species reaches a maximum height of 116 mm (BM 46444). However, in sandstones of the Margaritatus zone (Thorncombe Sands) in Dorset the relative proportions are reversed although the maximum height of *E. (E.) lunare* is only 37.5 mm (BM LL30727). In contemporaneous clays in Yorkshire *E. (E.) lunare* is greatly outnumbered by *C. (C.) subulatus* and reaches a maximum height of only 25 mm (author's collection). Apart from the above cases, *E. (E.) lunare*, although widespread, is only known to be common in the Gresten Beds of Austria (Trauth, 1909) where *Ch. (Ch.) textoria* and *Ps. (Ps.) dentatus* are also quite common.

8. INTERPRETATION OF ECOLOGY

It is clear from Section 7 that *E. (E.) lunare* exhibited considerable eurytopy with respect to substrate. However, if maximum size is taken as a measure of environmental favourability then, at least in the U. Pliensbachian, condensed ironstones can be seen to have offered more suitable conditions than sands or clays. This can presumably be explained, in the same way as suggested for *Ps. (Ps.) equivalvis* (see p. 71) by the reduced turbidity and possibly increased temperature characteristic of ironstone deposition. Specimens from the Sinemurian Arieten-Kalke which are not much smaller than those from the roughly contemporaneous Frodingham Ironstone may well be derived from condensed horizons within the predominantly argillaceous sequence (Urlichs, 1971).

If abundance is taken as a measure of environmental favourability then sandstones appear to have been just as suitable as ironstones. In both facies a frequent inverse correlation in the numbers of *E. (E.) lunare* and *Ps. (Ps.) equivalvis* is strong evidence for competition. In sandstones the dominant species appears to fluctuate at random from place to place but in ironstones *E. (E.) lunare* apparently lost its competitive superiority after the Sinemurian and *Ps. (Ps.) equivalvis* became dominant. There is no evidence for a similar competitive reaction with *Ps. (Ps.) dentatus, Ps. (Ps.) veyrasensis* or *Ch. (Ch.) textoria*.

Competition with *C. (C.) subulatus* is suggested by the tendency after the L. Sinemurian for *E. (E.) lunare* to be most abundant in arenaceous facies, a trend essentially opposite to that observed in the former species (q. v.).

Recent analogues of *E. (E.) lunare* are provided by species of *Amusium*. Most live in deep water (Knudsen, 1967) but some, such as *A. pleuronectes* and *A. japonicum*, migrate considerable distances into shallow water for the purpose of spawning (B. Morton, pers. comm., 1978). Swimming ability is excellent, with 'flights' of at least 10 m being possible, even at shell lengths near 100 mm. Stationary individuals recess into the sea bed.

9. FUNCTIONAL MORPHOLOGY

The small juvenile byssal notch and its subsequent allometric reduction in size imply that *E. (E.) lunare* could only have been byssally attached for a very short period early in ontogeny.

The large, smooth, low convexity shell is paradigmatic for reclining in the high energy environments favoured by the species. The dorsally extended auricles of the right valve may have assisted reclining in the same way as suggested for *Propeamussium (P.) laeviradiatum* (see p. 31). The thin shell is non-paradigmatic for reclining but probably represents an adaptation towards improved swimming efficiency, combined with ontogenetic increase in the umbonal angle. Smoothness and low convexity are also adaptive for swimming, but large size is not. However, bearing in mind the sizes at which swimming is possible in *Amusium* (see Section 8), it seems likely that the thinness of the shell offset any disadvantage resulting from the greater weight associated with large size.

Due to the rarity of bivalved specimens and generally poor preservation of the muscle scars, it has proved impossible to judge whether the high values for adductor muscle obliquity (Thayer, 1972) and moment (Gould, 1971) which contribute towards the considerable swimming ability of *Amusium*, are also characteristic of *E. (E.) lunare*.

The internal costae which presumably compensate for the reduced strength and stiffness of the smooth, non-plicate shell in *Amusium* would appear to be functionally represented by divaricate fibres within the shell of *E. (E.) lunare*.

10. ORIGINS AND EVOLUTION

Since *E. (E.) lunare* is first recorded in the Planorbis zone its origins probably lie in the Trias. *E. (E.) discites* (Schlotheim), a Trias species with a slight byssal notch seems to be the most likely ancestor.

There are no phyletic trends within *E. (E.) lunare* apart from a marked increase in maximum height in the same ironstone facies from 57 mm in the U. Sinemurian to 116 mm (possibly 145 mm, see Section 4) in the U. Pliensbachian. It should, however, be noted that the value of $3^{1}/_{2}$" (88 mm) cited for the "diameter" of Roemer's holotype from the Hettangian (Brauns, 1871) almost certainly implies a height greater than that attained in the U. Sinemurian, albeit in an isolated specimen.

The Toarcian decline of *E. lunare* may well be due to the widespread development of unfavourable bituminous shale facies in the lower substage. However, the fact that there appear to be at least a few U. Toarcian representatives (see Section 5) suggests that competition with *E. (E.) corneolum*, a species which apparently evolved in the latter substage, may also have played a part.

Entolium (Entolium) corneolum (Young and Bird 1828)

Pl. 1, Figs. 24–26, ? Figs. 20, 22, 27; text figs. 30–37

Synonymy

1828	? *Pecten corneolus* sp. nov; Young and Bird, p. 234, pl. 9, fig. 5.
v* 1829	*Pecten demissus* sp. nov; Phillips, pl. 6, fig. 5.
? 1833	*Pecten Phillipsii* sp. nov; Voltz in Thurmann, p. 32.
1833	*Pecten disciformis* sp. nov; Schübler in v. Ziften, p. 69, pl. 53, fig. 2.
pv? 1836	*Pecten cingulatus* sp. nov; Goldfuss, p. 74, pl. 99, figs. 3a, 3b.
? 1836	*Pecten subcomatus* sp. nov; Roemer, p. 70, pl. 3, fig. 17.
1836	*Pecten vitreus* sp. nov; Roemer, p. 72, pl. 13, fig. 7.
1836	*Pecten solidus* sp. nov; Roemer, p. 212, pl. 8, fig. 5.
1839	*Pecten spathulatus* sp. nov; Roemer, p. 26, pl. 18, fig. 22.
v non 1850	*Pecten disciformis* Schübler, d'Orbigny, v. 1, p. 237.
v? 1850	*Pecten Proeteus* sp. nov; d'Orbigny, v. 1, p. 257.
v* 1850	*Pecten silenus* sp. nov; d'Orbigny, v. 1, pp. 284, 314 (Boule, 1910, v. 5, p. 69, 1909, v. 4, pl. 20, fig. 12).
v* 1850	*Pecten Rhypheus* sp. nov; d'Orbigny, v. 1, p. 314 (Boule, 1913, v. 8, p. 92, pl. 2, figs. 24, 25).
v*? 1850	*Pecten subcingulatus* sp. nov; d'Orbigny, v. 1, p. 374 (Boule, 1927, v. 16, p. 132, 1928, v. 17, pl. 6, fig. 9).
v non 1852	*Pecten cingulatus* Goldfuss; Quenstedt, p. 506, pl. 40, fig. 41.
1853	*Pecten disciformis* Schübler; Chapuis and Dewalque, p. 21, pl. 31, fig. 2.
1855	*Pecten demissus* Phillips; Morris and Lycett, p. 127, pl. 14, fig. 7.
v* 1855	*Pecten censoriensis* sp. nov; Cotteau, p. 112.
v 1858	*Pecten demissus* Phillips; Quenstedt, pp. 353, 381, 553, pl. 48, figs. 6, 7, pl. 72, fig. 27.
v*? 1858	*Pecten demissus Gingensis* subsp. nov; Quenstedt, p. 378, pl. 51, fig. 1.
1858	*Pecten spathulatus* Roemer; Quenstedt, p. 433, pl. 59, fig. 13.
(?) 1858	*Pecten Renevieri* sp. nov; Oppel, p. 420.
1860	*Pecten Silenus* d'Orbigny; Coquand, p. 68.

1860 *Pecten demissus* PHILLIPS; COQUAND, p. 73.
1860 *Pecten solidus* ROEMER; COQUAND, p. 79.
1860 *Pecten demissus* PHILLIPS; DAMON, pl. 9, fig. 3.
? 1862 *Pecten Nicoleti* sp. nov; ÉTALLON in THURMANN and ÉTALLON, p. 263, pl. 37, fig. 5.
1862 *Pecten solidus* ROEMER; THURMANN and ÉTALLON, p. 262, pl. 37, fig. 5.
1862 *Pecten demissus* PHILLIPS; TRAUTSCHOLD, p. 2, pl. 7, figs. 2, 4 (non fig. 3).
non 1866 *Pecten demissus* PHILLIPS; LINDSTROM, p. 14, pl. 3, figs. 9, 10.
1867 *Pecten spatulatus* ROEMER; LAUBE, p. 9.
1867 *Pecten demissus* PHILLIPS; LAUBE, p. 10.
? 1867 *Pecten Gingensis* QUENSTEDT; WAAGEN, p. 627.
? 1867 *Pecten oblongus* sp. nov; WAAGEN, p. 629.
? 1869 *Pecten disciformis* SCHUBLER; DUMORTIER, p. 199.
1869 *Pecten cingulatus* GOLDFUSS; TERQUEM and JOURDY, p. 127.
1875 *Pecten solidus* ROEMER; DE LORIOL and PELLAT, p. 189, pl. 22, fig. 5.
? 1876 *Pecten Pilatensis* sp. nov; FAVRE, p. 65, pl. 7, fig. 3.
? 1881 *Pecten vitreus* ROEMER; DE LORIOL, p. 93, pl. 13, figs. 3–5.
1882 *Pecten (Entolium) vitreus* ROEMER; ROEDER, p. 56, pl. 2, figs. 2a, 2b, pl. 4, figs. 14a–d.
1883 *Pecten demissus* PHILLIPS; LAHUSEN, p. 24, pl. 2, fig. 4.
non 1883 *Pecten demissus* PHILLIPS; LUNDGREN, p. 16, pl. 2, fig. 12.
1883 *Pecten demissus* PHILLIPS; WHIDBORNE, p. 498.
? 1883 *Pecten demissus* var. *mutile* var. nov; WHIDBORNE, p. 499.
(?) 1883 *Pecten gingensis* QUENSTEDT; WHIDBORNE, p. 499.
? 1884 *Pecten disciformis* SCHUBLER; SIMPSON, p. 172.
(?) 1885 *Pecten (Amusium) Pilatensis* FAVRE; NICOLIS and PARONA, p. 45.
1886 *Pecten disciformis* SCHÜBLER; ROTHPLETZ, p. 36.
1888 *Pecten Rypheus* D'ORBIGNY; SCHLIPPE, p. 126, pl. 2, fig. 6.
1893 *Pecten (Entolium) cingulatus* GOLDFUSS; BOTTO-MICCA, p. 174.
1893 *Pecten vitreus* ROEMER; DE LORIOL, p. 312, pl. 33, fig. 8.
1893 *Chlamys (Pecten) vitrea* (ROEMER); SIEDMIRADZKI, p. 119.
1894 *Pecten (Entolium) disciformis* SCHÜBLER; MORICKE, p. 37.
1895 *Pecten vitreus* ROEMER; DE LORIOL, p. 45.
1896 *Pecten demissus* PHILLIPS; SEMENOW, p. 63.
1897 *Pecten vitreus* ROEMER; DE LORIOL, p. 129, pl. 16, figs. 5, 6.
? *1897* *Pecten demissus* PHILLIPS; POMPECKJ, p. 779.
? *1897* *Pecten disciformis* SCHUBLER; POMPECKJ, p. 779.
1898 *Pecten (Entolium) cingulatus* GOLDFUSS; GRECO, p. 109, pl. 8, figs. 30, 31.
1898 *Pecten (Entolium) disciformis* SCHÜBLER; TORNQUIST, p. 31.
1899 *Pecten demissus* PHILLIPS; SIMIONESCU, p. 215, pl. 2, fig. 6.
v 1903 *Pecten (Entolium) disciformis* SCHÜBLER; BURCKHARDT, p. 22, ? p. 8.
1904 *Pecten vitreus* ROEMER; ILOVAISKY, p. 251, pl. 8, fig. 13.
1905 *Pecten (Chlamys)* cf. *Rypheus* D'ORBIGNY; KILIAN and GUEBHARD, p. 743.
(?) *1905* *Pecten (Entolium) gingensis* QUENSTEDT; KILIAN and GUEBHARD, p. 743.
1905 *Pecten* cf. *disciformis* SCHÜBLER; KILIAN and GUEBHARD, p. 743.
1905 *Pecten (Entolium) demissus* PHILLIPS; KILIAN and GUEBHARD, p. 766.
1905 *Pecten (Entolium) solidus* ROEMER; KILIAN and GUEBHARD, p. 818.
v 1905 *Pecten censoriensis* COTTEAU; PERON, p. 232, pl. 10, figs. 5, 6.
1907 *Pecten demissus* PHILLIPS; DENINGER, p. 453.
1908 *Pecten (Entolium) vitreus* ROEMER; LEWINSKI, p. 435.
1910 *Entolium demissus* (PHILLIPS); LISSAJOUS, p. 363, pl. 10, figs. 7, 8.
1910 *Pecten (Entolium) demissus* PHILLIPS; RAVN, p. 463.
? 1910 *Pecten (Entolium) cingulatus* GOLDFUSS; RAVN, p. 464, pl. 33, fig. 7.
1911 *Pecten (Entolium) vitreus* ROEMER; BODEN, p. 193, pl. 7, figs. 17, 18.
1911 *Pecten (Entolium) disciformis* SCHUBLER; ROLLIER, p. 260.
? 1911 *Pecten (Entolium) Giengensis* sp. nov; ROLLIER, p. 260.
1911 *Pecten (Entolium) Silenus* D'ORBIGNY; ROLLIER, p. 260.
1911 *Pecten (Entolium) Rypheus* D'ORBIGNY; ROLLIER, p. 261.
1911 *Pecten (Entolium) spathulatus* ROEMER; ROLLIER, p. 262.
? 1911 *Pecten (Entolium) cingulatus* GOLDFUSS; ROLLIER, p. 263.
1915 *Pecten demissus* PHILLIPS; KRENKEL, p. 296.
non 1916 *Entolium disciforme* (SCHÜBLER); COSSMANN, p. 45, pl. 8, figs. 10, 11.
1916 *Pecten demissus* PHILLIPS; DOUVILLE, p. 75, pl. 10, fig. 2.
1917 *Pecten demissus* PHILLIPS; BORISSIAK and IVANOFF, p. 3, pl. 1, figs. 5, 8, 10, 15, 17.
1917 *Pecten spathulatus* ROEMER; BORISSIAK and IVANOFF, p. 6, pl. 1, fig. 13.
1917 *Pecten vitreus* ROEMER; BORISSIAK and IVANOFF, p. 8, pl. 1, figs. 1, 2, 12, 16 (non fig. 4).
1919 *Entolium silenus* (D'ORBIGNY); COSSMANN, p. 436.
1920 *Pecten solidus* ROEMER; FAURE-MARGUERIT, p. 55.
1923 *Pecten* cf. *vitreus* ROEMER; LEWINSKI, p. 60, pl. 2, fig. 11.
1923 *Syncyclonema demissum* (PHILLIPS); LISSAJOUS, p. 167.
1923 *Syncyclonema spathulatum* (ROEMER); LISSAJOUS, p. 168.
1924 *Entolium leachi* sp. nov; MCLEARN, p. 48, pl. 5, figs. 3, 11.
1924 *Pecten (Entolium) demissum* PHILLIPS; HENNIG, p. 14, pl. 2, figs. 1, 2.
v? 1926 *Entolium Proteus* (D'ORBIGNY); STAESCHE, p. 92, pl. 6, figs. 3, 4.
v 1926 *Entolium Renevieri* (OPPEL); STAESCHE, p. 93, pl. 3, fig. 4, pl. 6, fig. 6.
? 1926 *Entolium cingulatum* (GOLDFUSS); STAESCHE, p. 93, pl. 4, figs. 3, 4.
v 1926 *Entolium demissum* (PHILLIPS); STAESCHE, p. 99, pl. 4, fig. 5.
v? 1926 *Entolium Gingense* (QUENSTEDT); STAESCHE, p. 102, pl. 5, figs. 1, 2.
? 1926 *Entolium* aff. *solido* (ROEMER); STAESCHE, p. 103, pl. 3, figs. 13-15.
1926 *Entolium disciformis* (SCHÜBLER); ROMAN, p. 155.
1926 *Entolium spathulatus* (ROEMER); ROMAN, p. 168.
1926 *Entolium vitreus* (ROEMER); ROMAN, p. 198.
1929 *Pecten (Entolium) demissus* PHILLIPS; LANQUINE, p. 199.
1929 *Pecten (Entolium) valauryense* sp. nov; LANQUINE, p. 324, pl. 10, fig. 7.

v 1930a *Entolium demissum* (Phillips); Arkell, p. 91, pl. 7, fig. 4, pl. 9, fig. 8, text figs. 15–17.
1931 *Pecten (Camptonectes) vitreus* Roemer; Yin, p. 118.
1931 *Pecten (Entolium)* cf. *demissus* Phillips; Sokolov and Bodylevsky, p. 50, pl. 3, fig. 5.
(?) 1931 *Pecten (Entolium)* cf. *Nicoleti* Étallon; Sokolov and Bodylevsky, p. 52.
1932 *Entolium demissum* (Phillips); Spath, p. 112, pl. 26, fig. 2.
1933 *Pecten (Entolium) solidus* Roemer; Dietrich, p. 65, pl. 8, figs. 118, 119.
1934 *Pecten (Entolium) demissus* (Phillips); Stoll, p. 22, pl. 2, fig. 21.
? *1934* *Entolium demissum* (Phillips); Rosenkrantz, p. 117.
1935a *Entolium demissum* (Phillips); Arkell, p. x, pl. 53, fig. 3.
1935 *Pecten (Entolium)* cf. *demissus* (Phillips); Spath, p. 56.
? 1936 *Entolium cingulatus* (Goldfuss); Dechaseaux, p. 60.
1936 *Entolium disciformis* (Schübler); Dechaseaux, p. 61, pl. 8, figs. 12, 13.
1936 *Entolium demissus* (Phillips); Dechaseaux, p. 61.
(?) 1936 *Entolium Gingensis* (Quenstedt); Dechaseaux, p. 63.
1936 *Entolium spathulatus* (Roemer); Dechaseaux, p. 63.
? 1936 *Entolium* cf. *demissum* (Phillips); Wandel, p. 481.
1938 *Entolium demissum* (Phillips); Weir, p. 46, pl. 3, fig. 8.
non 1939 *Entolium disciforme* (Schübler); Stefanini, p. 177, pl. 19, fig. 15, pl. 20, fig. 1.
1939 *Entolium demissum* (Phillips); Stefanini, p. 179, pl. 22, figs. 2, 3.
1948 *Entolium corneolum* (Young and Bird); Cox and Arkell, p. 15.
1950 *Entolium corneolum* (Young and Bird); Channon, pp. 247, 248.
? 1951 *Entolium cingulatum* (Goldfuss); Troedsson, p. 217, pl. 20, figs. 1–3, pl. 21, figs. 11, 12.
1952 *Entolium demissum* (Phillips); Makowski, p. 17.
1954 *Pecten (Entolium) disciformis* (Schübler); Dean, p. 176.
1957 *Entolium leachi* McLearn; Frebold, p. 21.
1961 *Entolium* cf. *disciforme* (Schübler); Hayami, p. 255.
1961 *Entolium demissum* (Phillips); Barbulescu, pp. 701, 702.
1961 *Entolium* cf. *cingulatum* (Goldfuss); Barbulescu, p. 702.
non 1964 *Entolium cingulatum* (Goldfuss); Wellnhofer, p. 35, pl. 1, figs. 28–30.
1965 *Entolium corneolum* (Young and Bird); Cox, p. 51.
? 1965 *Entolium cingulatum* (Goldfuss); Cox, p. 52, pl. 6, fig. 15.
? *1966* *Entolium proteus* (d'Orbigny); Behmel and Geyer, p. 28.
? *1966* *Entolium demissus* (Phillips); Behmel and Geyer, p. 28.
? *1970* *Entolium cingulatum* (Goldfuss); Behmel, p. 62.
1971 *Entolium cingulatum* (Goldfuss); Barbulescu, p. 277.
? *1971* *Entolium proeteus* (d'Orbigny); Wendt, p. 156.
1971 *Entolium corneolum* (Young and Bird); Wendt, pp. 159, 161.
? *1971* *Entolium* cf. *cingulatum* (Goldfuss); Wendt, p. 160.
1971 *Entolium corneolum* (Young and Bird); Fürsich, p. 320.
? *1974* *Entolium cingulatum* (Goldfuss); Nitzopoulos, p. 46.
1975b *Entolium demissum* (Phillips); Hallam, p. 384.
1977 *Entolium demissum* (Phillips); Dietl, pl. 2, fig. 4.
1977 *Entolium demissum* (Phillips); J. Wright, p. 330.
1978 *Entolium (Entolium) corneolum* (Young and Bird); Duff, p. 62, pl. 4, figs. 25, 29, 30, pl. 5, figs. 3–5, text fig. 20.
1978 *Entolium corneolum* (Young and Bird); Brookfield, pp. 10, 15, 17, 26.

Neotype of *Pecten corneolus* Young and Bird 1828, p. 234, pl. 9, fig. 5 designated by Duff, 1978, p. 62; OUM J8151; figured Arkell, 1930a, pl. 7, fig. 4; H: 68, AL: 26, I_R: 41, HAA_R: 16.5, UA: 113; Osmington Oolite (M. Oxfordian), Malton, Yorkshire.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

'No. 5, also from the oolite, is smooth, brown, and thin like Sowerby's *P. corneus,* Tab. 204; but it is more oblong, and has smaller beaks. We may give it the name *P. corneolus.*'

2. AMENDED DIAGNOSIS

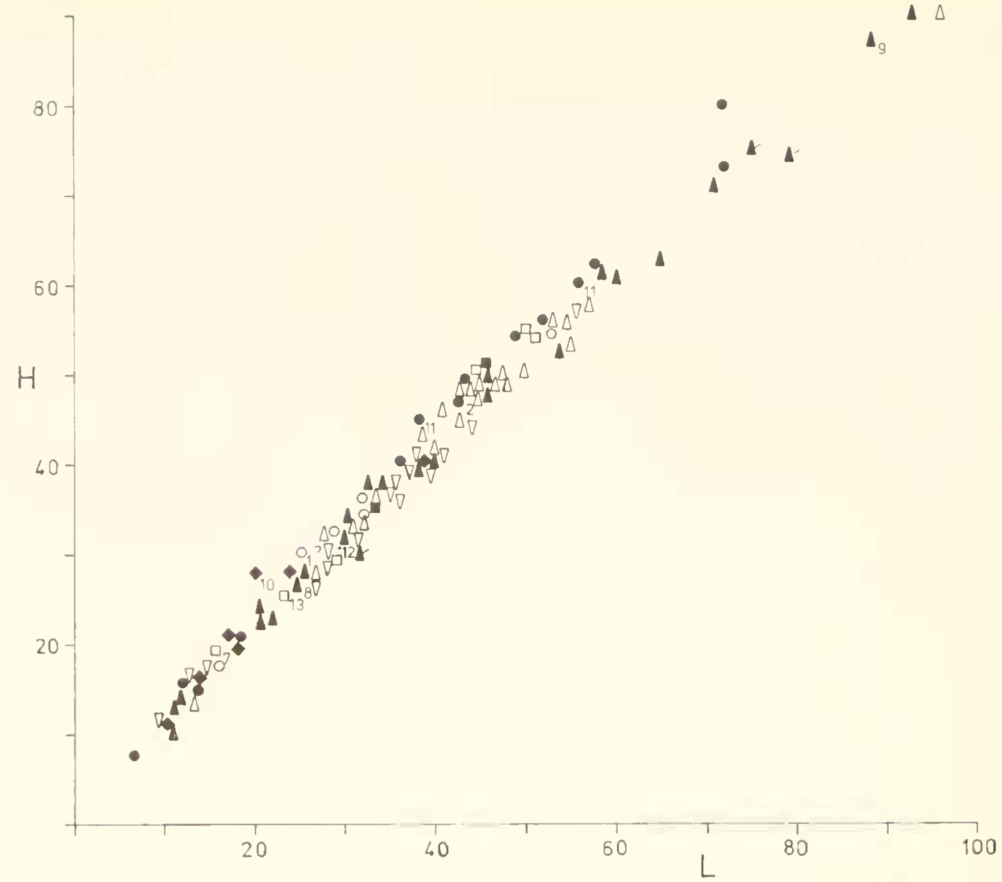
Distinguished from *E. (E.) lunare* by the lack of a byssal notch and from *E. (E.) orbiculare* by the lack of comarginal grooves on the right valve.

3. AMENDED DESCRIPTION

Essentially similar to *E. (E.) lunare,* differing by the diagnostic lack of a byssal notch (Pl. 1, Fig. 24), by the slower allometric reduction in H/L (text fig. 30), by the smaller maximum height (90 mm; NM, YM 531), by the slower rate of increase in umbonal angle, leading to generally higher H/UA values (text fig. 32), by the equality and isometric increase of the intersinal distance in both valves (text. figs. 33, 34), leading to much higher I/L values in the right valve, and by the isometric increase in height of the anterior auricle and probable allometric increase in the separation of the auricular apices, leading to higher values of HAA_R/L (text fig. 35) and AL/L (text fig. 31).

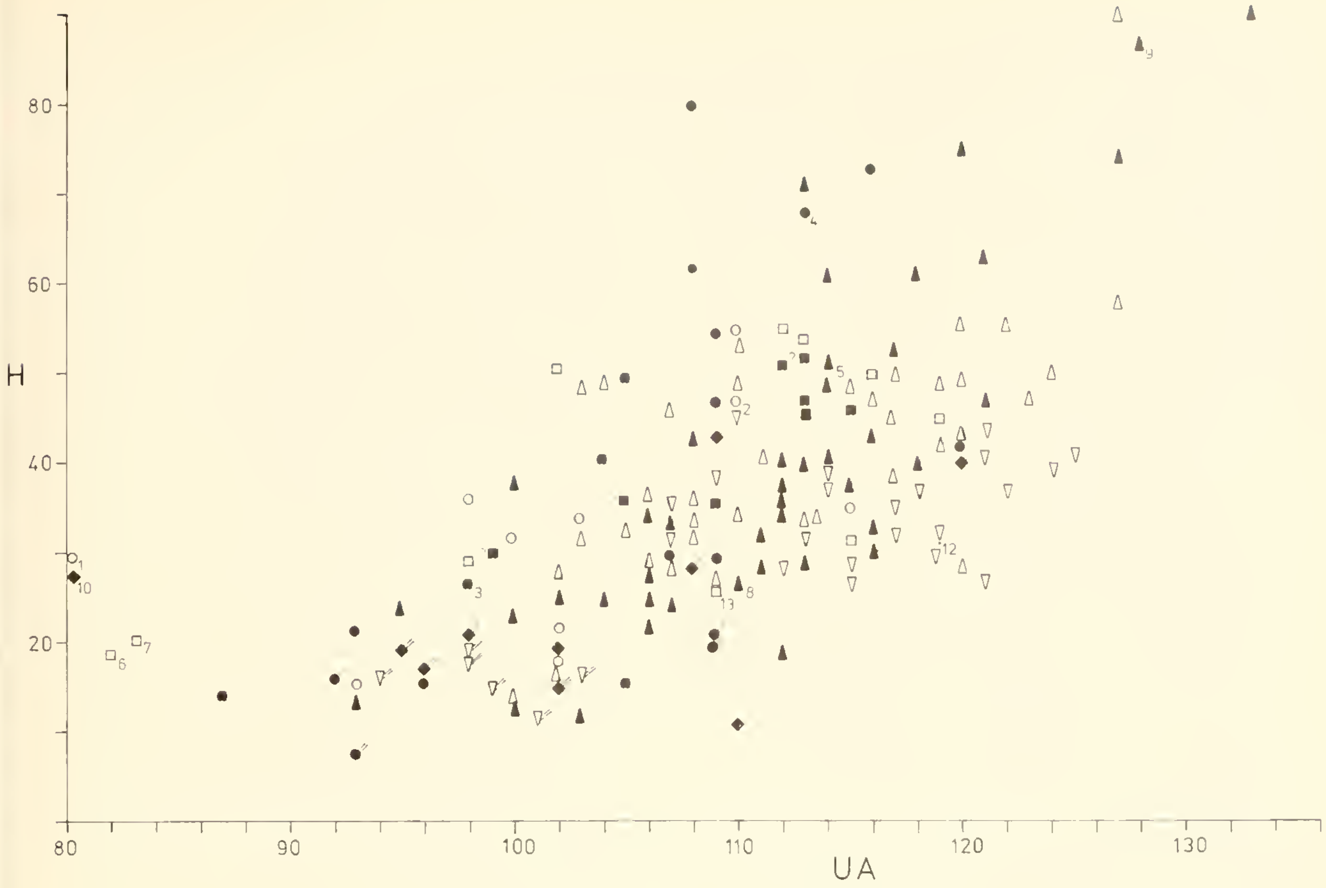
4. DISCUSSION

Examples of the species described in Section 3 have most often been referred to *'Pecten' demissus* Phillips. The sole known type (YM 202), a rather atypical form with a narrow umbonal angle (1), was said by Arkell (1930a) to exemplify Oxfordian forms of *Entolium* as distinct from Bajocian and Bathonian forms which were said to have a larger umbonal angle. Roemer's (1836) species *'P.' solidus* (2) and *'P.' vitreus* (3), also from the Oxfordian, were placed in synonymy with *'P.' demissus* on the basis of comparable umbonal angles. Arkell originally considered that Bajocian and Bathonian forms should be referred to d'Orbigny's (1850) species *'P.' Rhypheus* (syntypes [2] MNO 2908) but he later (1935a)



Text fig. 30: *Entolium (E.) corneolum* – height/length.

Text fig. 31: *Entolium (E.) corneolum* – separation of auricular apices/length.



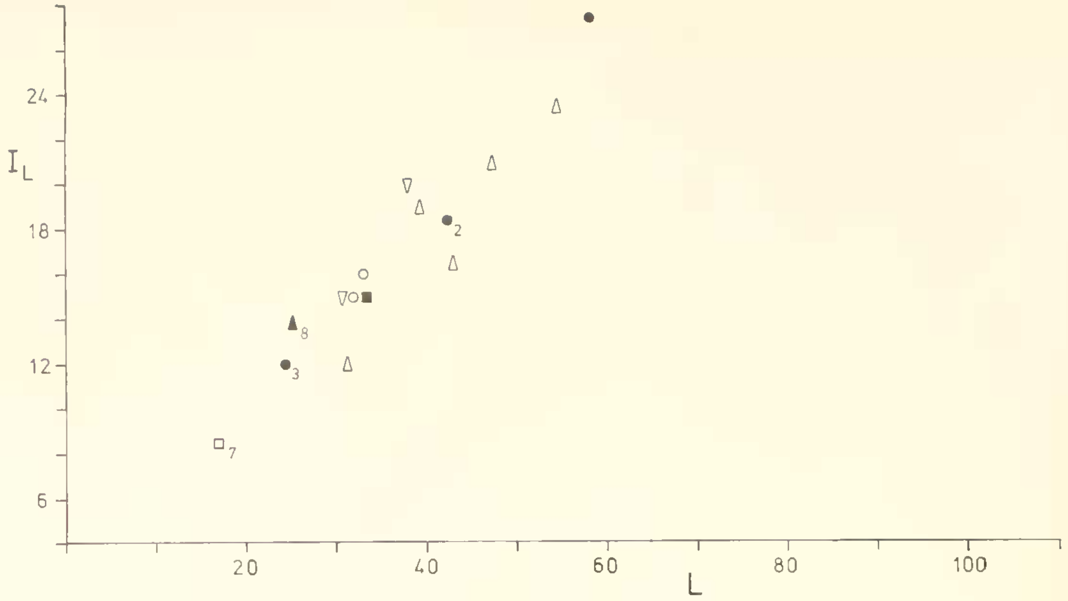
Text fig. 32: *Entolium (E.) corneolum* – heigth/umbonal angle.

considered that they should be united with forms referred to *'P.' demissus* (a conclusion supported by text fig. 32) under the slightly earlier name of *'P.' corneolus* Young and Bird (1828). The figure of the latter species is poor and the original is now lost. However, the description (see Section 1) leaves little doubt as to its affinities and Duff has now designated an appropriate neotype (OUM J8151; 4). Middle Jurassic representatives of *E. (E.) corneolum* have usually been referred to either *'P.' disciformis* Schübler or *'P.' spathulatus* Roemer. H/UA of the original figures of both species (5 and 6 respectively) from the M. Jurassic of Germany, is within the range of *E. (E.) corneolum* although that of *'P.' spathulatus* is near the limit of variation in measured specimens.

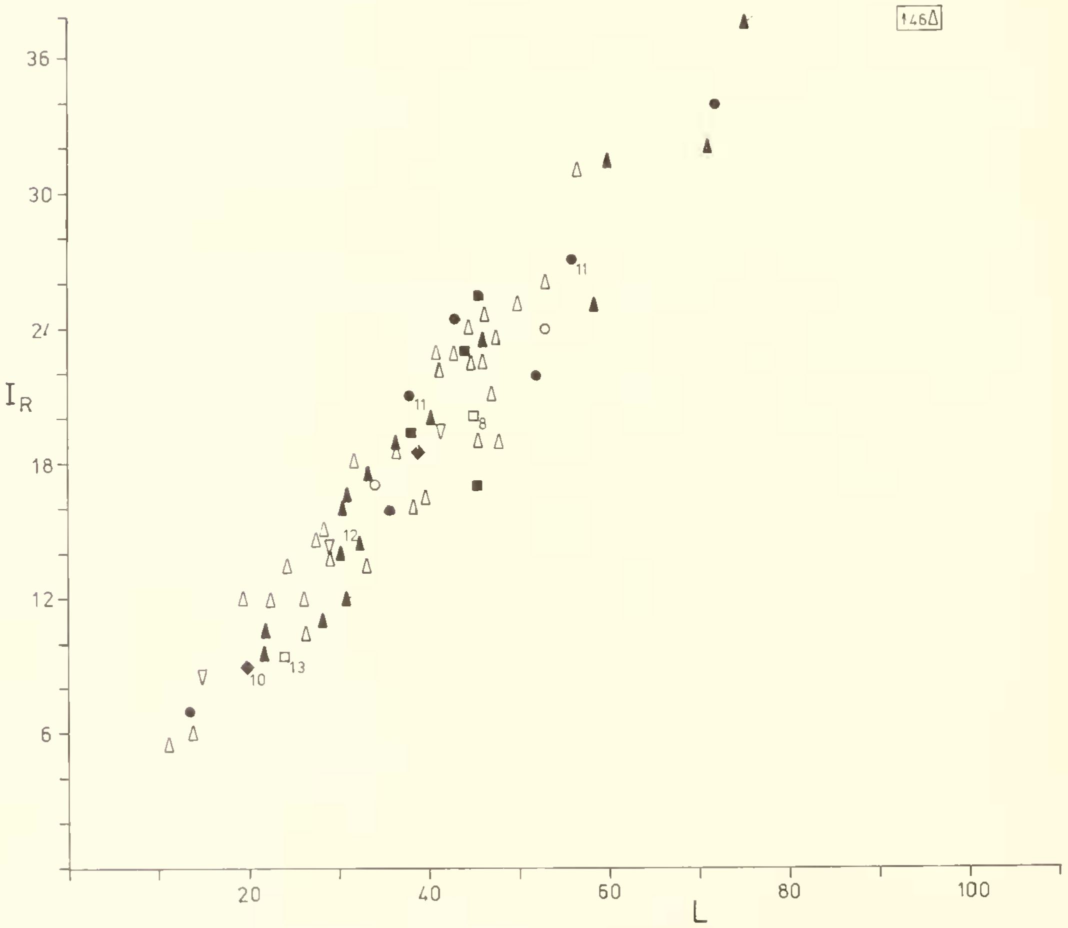
Lindstrom's (1866) and Lundgren's (1883) incorrect records of Phillips' species are discussed under *E. (E.) lunare*. Because of the possibility of confusion with the latter species in the Toarcian, unfigured records of Phillips' species from that stage in Pompeckj (1897), Rosenkrantz (1934), Wandel (1936), Dean (1954) and Behmel and Geyer (1966) must be treated with considerable caution. Unfigured Toarcian records of Schübler's species in Dumortier (1869), Simpson (1884), Pompeckj (1897), Burckhardt (1903) and Dechaseaux (1936) must be similarly treated. Pre-Toarcian figured specimens reffered to Schübler's species by d'Orbigny (1850) and Cossmann (1916) in fact belong to *E. (E.) lunare* as, most probably, do a number of unfigured specimens discussed under the latter species. Stefanini's (1939) figured specimen from the Bajocian of Somalia, referred to *E. (E.) disciforme*, exhibits quite pronounced radial ornament and is therefore not representative of *E. (Entolium)*. Trautschold's (1862, pl. 7, fig. 3) figured specimen from the Tithonian of Russia, referred to *'P.' demissus*, exhibits a large byssal notch and is probably an example of *Camptonectes*. Tausch's (1890) unfigured record of Roemer's *'P.' spathulatus* from the Toarcian of the S. Alps must be viewed with the same scepticism as other unillustrated records of *E. (E.) corneolum* from the stage. De Loriol's (1881) illustrated record of Roemer's *'P.' vitreus* and Staesche's (1926) illustrated record of Roemer's *'P.' solidus* both refer to specimens with rather pronounced comarginal ornament which may thus be referable to *E. (E.) orbiculare*.

Borissiak and Ivanoff's (1917, pl. 1, fig. 4) figure of *'P.' vitreus* depicts a specimen with a slight byssal notch which is thus not referable to *E. (E.) corneolum*. In the present state of knowledge (see p. 36) it is impossible to say whether it should be referred to *E. (E.) lunare* or *E. (E.) orbiculare*.

'P.' subcomatus Roemer from the Bathonian has H/UA (7) only just within the range of *E. (E.) corneolum* and until the type material is examined the possibility cannot be entirely excluded that the divaricate lines on the figure are in fact representative of the divaricate striae of *Camptonectes (C.) laminatus*. The fine radial striae on a syntype of *'P.' subcingulatus* d'Orbigny (MNO 3763) from the Oxfordian suggest that the species is referable to *Propeamussium*, despite its en-



Text fig. 33: *Entolium (E.) corneolum* – intersinal distance on left valve/length.



Text fig. 34: *Entolium (E.) corneolum* – intersinal distance on right valve/length.

tolioid form. However, the syntypes of *'P.' silenus* d'Orbigny (MNO 2904) are completely smooth and have metric proportions (8) well within the range of *E. (E.) corneolum*.

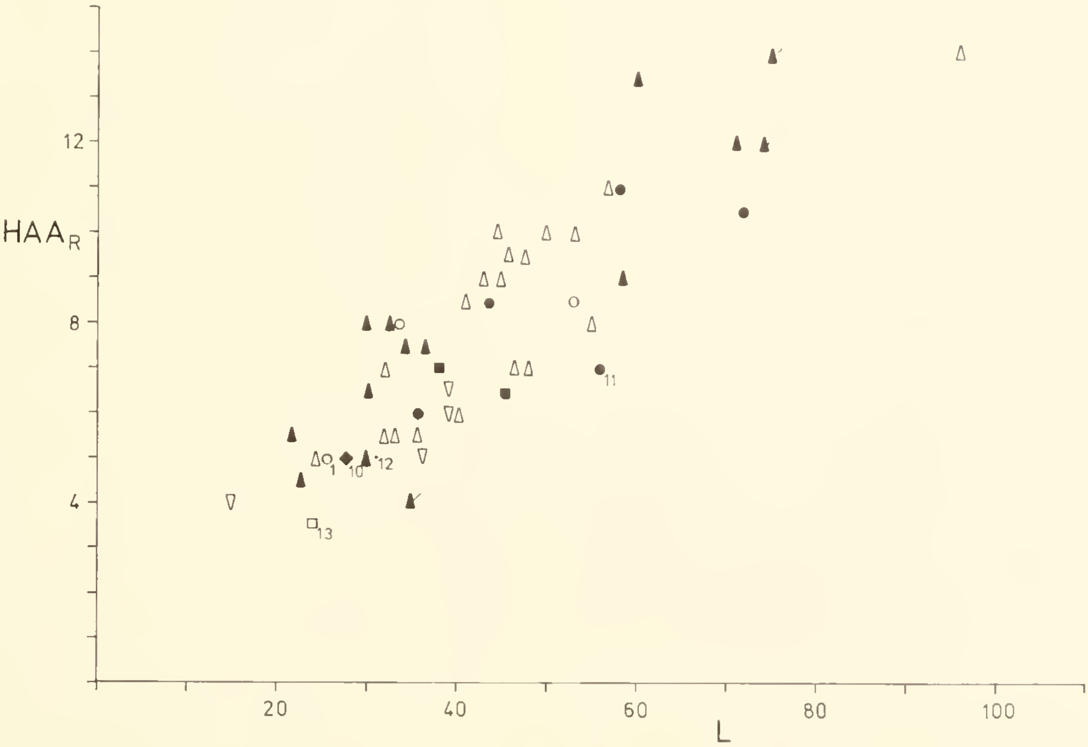
The subspecies *'P.' demissus Gingensis* Quenstedt was erected for a large specimen (GPIT) from the Bajocian of Gingen (S. Germany) with large, symmetric auricles. Apart from I_L/L all metric proportions (9) plot within the range of *E. (E.) corneolum* and the absence of intermediate sized specimens precludes any assessment of whether the large I_L/L (54/88) is the product of some hitherto undetected allometry or is indicative of a more profound difference. Topotype specimens (identified with a glyph) of which only five are known (GPIT, GPIG [3], MNS) plot within the range of *E. (E.) corneolum* projected to larger sizes but have strong auricular crura and thick shells (Pl. 1, Fig. 27) which may justify Waagen's (1867) elevation of the subspecies to specific rank. Waagen erected a further species, *'P'. oblongus*, for forms with large auricles from the Bajocian of Gingen. Although unillustrated it seems quite possible that they are synonymous with *'P.' Gingensis*, if not with *E. (E.) corneolum*. Whidborne (1883) recorded a further unfigured specimen of *'P.' gingensis* from the Northampton Sand Ironstone (Aalenian) and also created the variety *inutile* for forms of *'P.' demissus* with large auricles. It seems likely that they too are representative of *'P.' Gingensis*. Whidborne's variety *celatus* was said to have radiating lines and may therefore be representative of *Propeamussium* rather than *E. (Entolium)*.

The figure of *'P.' Nicoleti* Étallon (?holotype: École cantonale de Porrentruy [Wannier and Panchaud, 1977]) from the Kimmeridgian of Switzerland has extremely high H/L and H/UA (10) but at least with respect to the latter parameter it is comparable to the single type of *'P.' demissus* Phillips (1) and may therefore be no more than a narrow form of *E. (E.) corneolum*.

'P.' Pilatensis Favre, from the Oxfordian of Switzerland, was compared with *'P.' demissus* and *'P.' vitreus* but has rather strong comarginal ornament and thus may be representative of *E. (E.) orbiculare* rather than *E. (E.) corneolum*.

The syntypes of *'P'. censoriensis* Cotteau (MNS B. 03983; Pl. 1, Fig. 26) from the Oxfordian of the Yonne can only be distinguished from *E. (E.) corneolum* by a somewhat low HAA_R/L (11). Since only two specimens are available it seems unwise to regard them as specifically distinct. Likewise it seems improper to separate *E. leachi* McLearn on the basis of a somewhat low H/UA (12) when all other proportions of the figured specimen are similar to those of typical representatives of *E. (E.) corneolum*. Metric proportions of *'P.' (E.) valaurycnse* Lanquine (13) from the Bathonian of Provence, are entirely within the range of *E. (E.) corneolum*.

Goldfuss (1836) apparently based his concept of *'P.' cingulatus* on a specimen from the Oxfordian figured by Phillips (1829, pl. 5, fig. 11) as *'P.'* sp. The latter possesses a slight byssal notch and may be a late representative of *E. (E.) lunare* (q. v.). However additional figures of *'P.' cingulatus* provided by Goldfuss show no sign of a byssal notch and are not dissimilar to *E. (E.) corneolum*. What may be regarded as paratypes in the GPIB (610a, 610b) could certainly be taken to be representatives of *E. (E.) corneolum*. However, comarginal ornament is quite strongly developed (Pl. 1, Figs. 20, 22) and this, together with the fact that the example figured in Pl. 1, Fig. 22 has a smooth opposite valve, suggests that the specimens may possibly be representative of *E. (E.) orbiculare* (cf. Pl. 1, Fig. 19). Goldfuss cited localities in both the L. and U. Jurassic for his species, thus his hypodigm could well have included *E. (E.) lunare* in addition to one or other of *E. (E.) corneolum* and *E. (E.) orbiculare*. However, d'Orbigny (1850) subsequently created *'P.' Philenor* and *'P.' Proteus* for L. Jurassic forms which he would otherwise have assigned



Text fig. 35: *Entolium (E.) corneolum* – height of anterior auricle on right valve/length.

to '*P.*' *cingulatus* and, following Staesche (1926), Cox (1952, 1965) has taken this to imply a restriction of Goldfuss' hypodigm to U. Jurassic forms. It should be noted in passing that Dechaseaux (1936) and Troedsson (1951) have applied Goldfuss' specific name to L. and M. Liassic forms of *E. (Entolium)* which are, in consequence of the horizon of derivation, very probably representative of *E. (E.) lunare*. Examples of *E. (Entolium)* from U. Jurassic marls in S. Germany, whence some of Goldfuss' paratypes were derived, appear to be distinguishable from *E. (E.) corneolum* (the *E. (Entolium)* species usually encountered elsewhere at this time) by a low UA. However, text fig. 32, in which these specimens are identified with a double glyph, shows that this is an illusion created by small size. Nevertheless, certain specimens collected by Wellnhofer (1964) from marls in the U. Jurassic of S. Germany probably differ from *E. (E.) corneolum* in the possession of internal ridges (see p. 36) and it could be that Goldfuss' paratypes are similarly distinct. The affinities of Goldfuss' species are thus extremely uncertain and while it seems likely that most authors would apply the name *cingulatus* to specimens referable to *E. (E.) corneolum* there remains the possibility for U. Jurassic forms that Goldfuss' specific name could be applied to *E. (E.) orbiculare* or to the probably separate species with internal ridges. Specimens figured by Ravn (1910) and Cox (1965) appear similar to Wellnhofer's material while specimens referred to *E. cingulatum* by Staesche (1926), apparently with strong comarginal ornament, may be representative of *E. (E.) orbiculare*. However, unillustrated U. Jurassic specimens referred to Goldfuss' species by Rollier (1911), Behmel (1970), Wendt (1971) and Nitzopoulos (1974) are of completely indeterminate affinities. Since neither the 'species' with internal ridges nor *E. (E.) orbiculare* are known definitely to occur before the U. Jurassic, unillustrated M. Jurassic records of Goldfuss' species in Terquem and Jourdy (1869), Botto-Micca (1893) and Barbulescu (1961, 1971), together with Greco's (1898) poorly illustrated record, can be ascribed with some confidence to *E. (E.) corneolum*. The specimen (GPIT 4-74-10; Pl. 1, Fig. 11) figured by Quenstedt (1852) as '*Pecten*' *cingulatus* (accorded the name '*P.*' *cornutus* by Quenstedt in 1858) has extremely extended auricles on the right valve and in this respect resembles *Propeamussium (P.) laeviradiatum* (see however p. 29). It is possible (see p. 41) that some of the specimens referred to d'Orbigny's (1850) replacement specific name *('P.' Proeteus)* for Toarcian '*P.*' *cingulatus* may belong to *E. (E.) corneolum* and Wendt's (1971) record from the Aalenian and Bajocian of Sicily almost certainly refers to the latter species.

'*P.*' *Renevieri* Oppel was erected for an unfigured specimen from the Bajocian of S. Germany said to generally resemble '*P.*' *cingulatus* but to differ by stronger comarginal ornament. The density of the latter (12 per half inch) is probably too high to suggest that '*P.*' *Renevieri* is an exceptionally early representative of *E. (E.) orbiculare* and a specimen (GPIT) from the same stage and region, referred to Oppel's species by Staesche (1926), appears to be a form of *E. (E.) corneolum* in which growth has been periodically halted, resulting in a regular arrangement of strong growth lines.

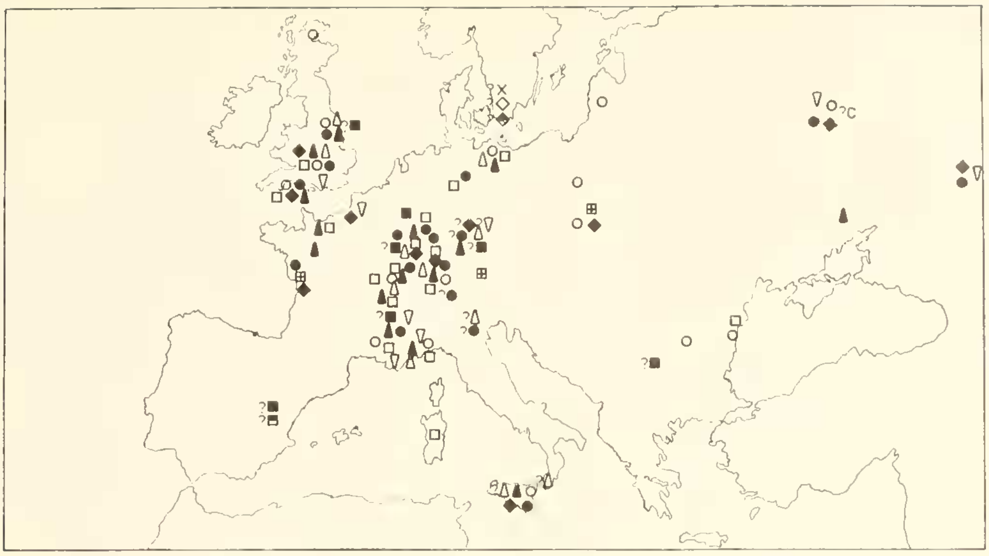
'*P.*' *Phillipsii* Voltz proposed, like '*P.*' *cingulatus* Goldfuss, for '*P.*' sp. Phillips and applied to unfigured Bathonian specimens from E. France, is almost certainly referable to *E. (E.) corneolum*. It should be noted that Voltz's species (published in 1833) becomes a senior objective synonym of Goldfuss' species if the latter is taken to include the original of '*P.*' sp. Phillips (see above). It should be further noted that following the ambiguous statement in Goldfuss many authors (e. g. Quenstedt, 1852; Terquem and Jourdy, 1869; Greco, 1898) have incorrectly ascribed the authorship of '*P.*' *cingulatus* to Phillips (1829).

In the interests of brevity unfigured secondary records of synonymous and probably synonymous species which are of no relevance to Sections 4-10 are excluded from the synonymy. They may be found in the following works: for '*P.*' *corneolus*, Channon (1950); for '*P.*' *demissus*, Bean (1839), Quenstedt (1843), d'Orbigny (1850), v. Seebach (1864), Schlippe (1888), Paris and Richardson (1916), Roman (1926), Barbulescu (1971); for '*P.*' *disciformis*, v. Buch (1839), Oppel (1858),, v. Seebach (1864), Waagen (1867), Deninger (1907), Lanquine (1929), Barbulescu (1961); for '*P.*' *vitreus*, de Loriol (1894, 1901, 1904), Sokolov and Bodylevsky (1931); for '*P.*' *solidus*, d'Orbigny (1850), Arkell (1926); for '*P.*' *spathulatus*, Terquem and Jourdy (1869), Barbulescu (1971); for '*P.*' *silenus*, Fürsich (1971); for '*P.*' *Gingensis*, Deninger (1907), Lanquine (1929); for '*P.*' *Renevieri*, Rollier (1911), Fürsich (1971); for '*P.*' *Nicoleti*, Siemiradzki (1893); for '*P.*' *Valauryense*, Dechaseaux (1936).

5. STRATIGRAPHIC RANGE

The earliest records of *E. (E.) corneolum* are provided by six specimens (GPIG) from the Toarcian of Esch, Luxembourg which lack a byssal notch, have high H/UA ratios and exhibit the large auricles (Pl. 1, Fig. 25) typical of the species. From the ironstone matrix it is reasonable to conclude that the specimens are derived from the U. Toarcian strata in the area. A specimen (GPIG) from the same horizon at Heiningen, S. Germany has the ovate form more characteristic of *E. (E.) corneolum* than *E. (E.) lunare* while two specimens from the U. Toarcian of Somerset (BM L42004, L74597) and a further specimen from undifferentiated Toarcian in Warwickshire (BM 66789) have the high H/UA ratios typical of *E. (E.) corneolum*. A number of poorly preserved specimens from undifferentiated Lias in S. America (GPIG) have a narrow form highly reminiscent of *E. (E.) corneolum*. Specimens from the Toarcian which have poorly preserved auricles and which therefore cannot confidently be assigned to a species are prefixed by a question mark in text fig. 32. Bibliographic records from the Toarcian of species which are considered herein to be synonymous with *E. (E.) corneolum* are all equivocal (see Section 4). However, it is perhaps worth noting that Dumortier's (1869) and Behmel and Geyer's (1966) citations are of specimens from the Bifrons Zone (L. Toarcian).

E. (E.) corneolum becomes common and locally abundant in the Aalenian and continues thus until the uppermost Jurassic (Trautschold, 1862; de Loriol and Pellat, 1875; Yin, 1931; ?Kilian and Guébhard, 1905). Specimens from the U. Volgian of Moscow (GPIG; Borissiak and Ivanoff, 1917) probably indicate that *E. (E.) corneolum* survived into the Cretaceous.



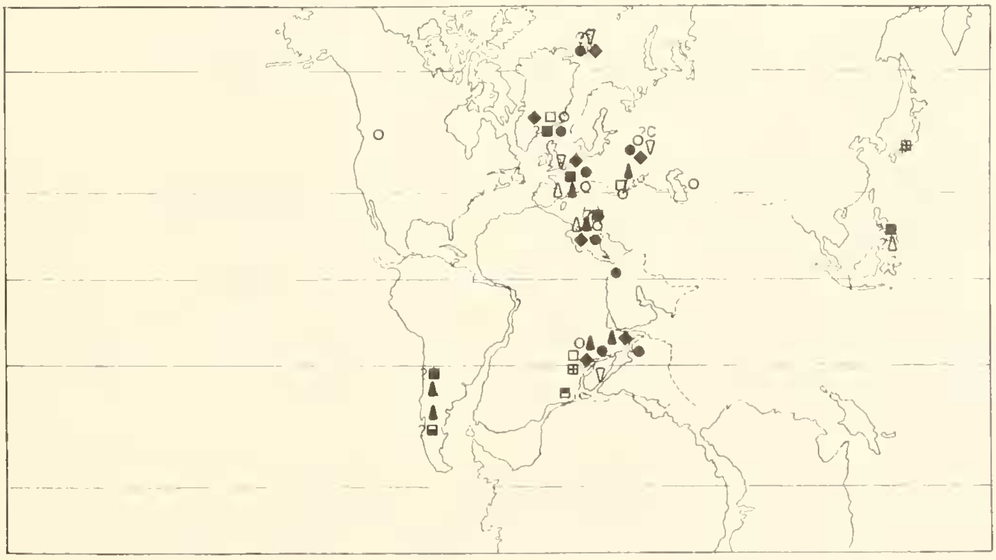
Text fig. 36: *Entolium (E.) corneolum* – European distribution.

6. GEOGRAPHIC RANGE

Unequivocal Toarcian records of *E. (E.) corneolum* are restricted to Europe (text fig. 36) and the same may also be true in the Aalenian; Wandel's (1936) record from that stage in the E. Indies being of an unfigured specimen which was merely compared with Phillips's synonym (*'P.' demissus*) of *E. (E.) corneolum*. Subsequently the species spread to many parts of the world resulting, by the U. Jurassic, in a palaeolatitudinal range approaching 100° (text fig. 37). Outside Europe *E. (E.) corneolum* is, however, only known to be common in the Bajocian of the Andes (Tornquist, 1898) and the Oxfordian/L. Kimmeridgian of E. Greenland (Spath, 1935) and the species is notably absent from the U. S. Western Interior where the reduced diversity fauna, in which *Camptonectes* is the only common pectinid, is suggestive of high environmental stress (Hallam, 1975a). McLearn's (1924) record of common specimens from undifferentiated Jurassic in Alberta may well be from the Callovian, bearing in mind Frebold's (1957) use of McLearn's synonym (*E. leachi*) of *E. (E.) corneolum* for specimens from that stage.

7. DESCRIPTION OF ECOLOGY

E. (E.) corneolum first occurs commonly in the chamosite oolites of the Northampton Sand Ironstone (Aalenian; Opalinum zone) where it reaches a maximum height of 53 mm (author's collection) and is associated with a diverse bivalve fauna (see p. 26) including *Propeamussium (P.) pumilum* but lacking *P. (P.) laeviradiatum*. In a similar sedimentary and faunal association in the Murchisonae zone of S. Germany *E. (E.) corneolum* is abundant and reaches a maximum height of 58 mm (GPIT) while in the Aalenian of Lorraine the species is common in chamosite oolites of the Opalinum zone and reaches a maximum height of 90 mm (NM) in ironshot sediments probably of the Concavum zone. *E. (E.) corneolum* occurs in a variety of limestones (including



Text fig. 37: *Entolium (E.) corneolum* – World distribution (Callovian reconstruction).

those bearing corals [Channon, 1950]) in the Aalenian of the Cotswolds (reaching a maximum height of 49 mm [OUM J34471]) and near Yeovil it occurs commonly in ironshot oolites. In similar sediments in Provence *E. (E.) corneolum* reaches a maximum height of 74 mm (Lanquine, 1929).

In the L. Bajocian of S. Germany *E. (E.) corneolum* attains a maximum height of 40.5 mm (GPIT) and is particularly abundant in the Blaukalke, a sandy limestone (Staesche, 1926). Specimens from the Sowerbyi-Banke which are referable to the possibly synonymous species '*P.*' *Gingensis* Quenstedt (see Section 4) attain a maximum height of 87 mm (GPIT) but specimens which are definitely referable to *E. (E.) corneolum* attain a maximum height of 90 mm (YM 531) in the contemporaneous Millepore Bed, a sideritic sandstone in Yorkshire (fauna p. 123). Only one specimen (GPIG) is known from the relatively restricted fauna (indicative of lower environmental stability) in the somewhat later Scarborough Beds of the same area. In the L. Bajocian of E. France *E. (E.) corneolum* occurs quite frequently in inter-reef biosparites and biomicrites (Hallam, 1975b).

In the U. Bajocian of S. Germany the species is reported to be abundant (Staesche, 1926) and reaches a maximum height of 41 mm (GPIT). It is also common in condensed ironshot oolites in Normandy while contemporaneous specimens from limestones in the Cotswolds are common and attain a maximum height of 71 mm (BM LL15). The species is reported to be common in Bajocian dolomitised oolites in the Maritime Alps (Kilian and Guébhard, 1905).

Records of common L. Bathonian specimens of *E. (E.) corneolum* are restricted to the Mâconnais (Lissajous, 1923) and the species is not known to be common again until the uppermost Bathonian (Discus zone) when it is found in the shell fragment limestones of the L. Cornbrash in England (fauna p. 128), attaining a maximum height of 55 mm (OUM J7135). All the specimens cited by Cox and Arkell (1948) from the marginal marine facies of the Bathonian in central England appear to be representatives of *Camptonectes* (M. J. Bradshaw, pers. comm., 1977) and the majority of Bathonian records of *E. (E.) corneolum* are in fact concentrated in central and southern Europe (text figs. 36, 37).

In the L. Callovian (Macrocephalus zone) *E. (E.) corneolum* is abundant in the chamosite oolith-bearing limestones of the U. Cornbrash in Yorkshire and attains a maximum height of 55 mm (SbM H 73.4). In the immediately overlying Shales of the Cornbrash the species is reported to be abundant (J. Wright, 1977) but all specimens discovered by the author have been small (H: <30). In the same area similar specimens (H_{max}: 36.5; BM 47433) are fairly common in the low diversity benthic fauna (see p. 208) of sandstones forming the Kellaways Rock (Calloviense zone) and chamosite oolites forming the Hackness Rock (U. Callovian; Athleta and Lamberti zones) both of which were probably deposited very near shore (J. Wright, 1978). Small specimens also occur in the more basinal non-bituminous shales of the L. and M. Callovian in E. Scotland and U. Callovian of E. England (Duff, 1978). However, in the predominantly bituminous shales of the L. and M. Callovian in the latter area *E. (E.) corneolum* is not only small but is restricted to a subordinate role in shell beds which contain, in comparison to contiguous deposits, a relatively high proportion of suspension feeding bivalves (Duff, 1975). Kilian and Guébhard (1905) report the species as common in thin-bedded limestones containing numerous suspension feeding bivalves in the Callovian of S. France while Lewinski (1908) reports common examples in marls of the same age in Poland.

Roeder (1882) reports common *E. (E.) corneolum* in the L. Oxfordian 'Terrain à Chailles' of Alsace (fauna pp. 88, 208) and Peron's (1905) record of common Oxfordian specimens from the same area may well be from this horizon rather than the coral-bearing limestones of the U. Oxfordian. However, the latter facies seems to support fairly common *E. (E.) corneolum* in the Swiss Jura (de Loriol, 1893) where the species reaches a maximum height of 77 mm (de Loriol, 1895). Similar sediments in the Oxfordian of N. Germany (Roemer, 1836) and England (Arkell, 1930a; Brookfield, 1978) also contain *E. (E.) corneolum* up to a maximum height of 80 mm (YM 560). However the species is not particularly common, forming no part of the trophic nuclei of any of Fürsich's (1977) faunal associations, and according to Arkell (1928) it is largely restricted to inter-reef biosparites. Specimens from Oxfordian marls and biomicrites in S. Germany reach a maximum height of only 21 mm (GPIT) but if Nitzopoulos' (1974) information is taken to refer to *E. (E.) corneolum* (see Section 4) the species is fairly common in an otherwise sparse benthic fauna. In similar sediments in the Kimmeridgian of the same area *E. (E.) corneolum* attains a maximum height of 28.5 mm (GPIT) but here, as in other occurrences in the stage, there is no evidence of anything more than a few specimens although the species is widespread (text fig. 36). An isolated specimen from unknown facies in Russia has a height of 45 mm (BM L4170). *E. (E.) corneolum* is absent from Oxfordian sands in Normandy, (Chavan, 1952), together with Kimmeridgian marls in N. W. Germany (Huckriede, 1967) and limestones in Poland (Alth, 1882) where the presence of euryhaline bivalve genera and paucity of ammonites is suggestive of abnormal salinities. By contrast, in the L. Tithonian ammonite-bearing marly limestones of the last area *E. (E.) corneolum* is very common (Lewinski, 1923). In the M. Tithonian (Pectinatus zone) near Oxford *E. (E.) corneolum* is also very common, reaching a maximum height of 57 mm (OUM J14519). Many specimens have somewhat low H/UA ratios as in the co-occurring *Camptonectes (C.) auritus*. *E. (E.) corneolum* occurs with *E. (E.) orbiculare* in the U. Jurassic of Moscow (GPIG) and Spitzbergen (Sokolov and Bodylevsky, 1931).

The wide variety of sediments in which *E. (E.) corneolum* is found in large numbers, of which all known European examples are described above, is also occupied by somewhat fewer individuals at many other horizons in the M. and U. Jurassic. However, the low diversity faunas of basinal argillaceous sediments in the peri-Mediterranean region do not appear to contain *E. (E.) corneolum* except possibly in the U. Jurassic of E. Spain where Behmel (1970) records as the most common fossil the questionably synonymous species *E. cingulatum* (see Section 4). All other records from the region are either from faunally rich neritic facies or from somewhat reduced diversity, condensed, fine-grained swell facies where the species seems to be small in size (e. g. Botto-Micca, 1893).

8. INTERPRETATION OF ECOLOGY

If assessed in terms of its abundance it is clear from Section 7 that *E. (E.) corneolum* was a remarkably eurytopic species with respect to substrate. Certain clay-grade sequences where the low density and diversity of other suspension feeding bivalves is indicative of high turbidity or soupy substrates seem to have constituted the only unfavourable environments and even these *E. (E.) corneolum* may have been able to colonise in large numbers locally. However, if assessed in terms of its size it is clear that expanded sequences of argillaceous sediments did not provide the most suitable substrates for *E. (E.) corneolum*, individuals from such facies being always smaller than those from contemporaneous deposits of arenaceous grade. In the latter the large size of specimens from sequences where the precipitation of siderite and chamosite is indicative of slow sedimentation suggests that the development of firm substrates and low turbidity was conducive to rapid growth and the attainment of large size. Further support for the importance of the last factor is provided by the occurrence of large specimens in arenaceous sediments close to coral reefs, the growth of which is inhibited by high turbidity. The high environmental energy associated with arenaceous sedimentation was, by the evidence of the reduced size of specimens from expanded compared to contemporaneous condensed sequences, apparently insufficient on its own to promote rapid growth. In fact, the relatively reduced H/UA of specimens from an expanded sand sequence in the M. Tithonian suggests that growth was actively retarded in such sequences. In the lack of any M. Tithonian occurrences of *E. (E.) corneolum* from condensed facies, it is impossible to rule out the possibility that the H/UA decrease is a phyletic effect (see Section 10). However, the parallel change in the ecologically distinct but co-occurring *Camptonectes (C.) auritus* argues strongly for stunting. The relative abundance of medium to small specimens in this and other expanded arenaceous and argillaceous sequences need not be viewed as evidence against stunting (see p. 124 and Hallam, 1965).

In contrast to its considerable substrate eurytopy *E. (E.) corneolum* seems to have been unable to tolerate environments where the low faunal diversity is indicative of abnormal salinity or the more general instability of marginal marine situations. Sequences which were largely deposited under conditions of reduced oxygen tension were only colonised, and then rarely, at horizons where the development of shell beds suggests a brief replacement of stagnant by more acitve and oxygenated conditions.

There is no evidence for any competitive reaction with the morphologically very similar species *E. (E.) orbiculare*, nor with *Propeamussium (P.) pumilum* and *P. (P.) nonarium*. However *E. (E.) corneolum* is very rarely found with *P. (P.) laeviradiatum* despite the favourability for the former species of the condensed facies to which the latter is restricted. It seems likely that a similar mode of life (see Section 9) may have led to mutual competitive exclusion.

Very close Recent morphological analogues of *E. (E.) corneolum* are described on p. 45).

9. FUNCTIONAL MORPHOLOGY

Apart from the absence of a byssal notch *E. (E.) corneolum* is in all relevant aspects of morphology identical to *E. (E.) lunare*. A similar mode of life, differing only by the lack of a byssate juvenile phase, can therefore be inferred (see p. 45). *E. (E.) corneolum* has a lower rate of increase in umbonal angle so swimming ability may have been somewhat impaired at large sizes. The small maximum size of individuals colonising soft argillaceous substrates is adaptive in that it minimises sinking into the substrate. Stunting, with its implication of inadaptiveness, may therefore be an inappropriate term to apply to the development of small size in such environments (see Section 8).

10. ORIGINS AND EVOLUTION

E. (E.) lunare is the only known candidate for the ancestor of *E. (E.) corneolum* in the Jurassic. All the differences displayed by the latter species can be explained by the heterochronic alteration of the ontogeny of the former. However, simultaneous retardation (for H/L, I_R/L, HAA/L and AH/L) and acceleration (for H/UA and the lack of a byssal notch) of the development of the components of shape with respect to size would have to be invoked and it is by no means certain whether such a situation could arise in a single speciation event. It may be that an as yet undetected species is the direct ancestor of *E. (E.) corneolum*.

The undoubted existence of ecophenotypic variation in size and the lack of adequate collections from any one facies throughout the stratigraphic range of *E. (E.) corneolum* makes for great difficulty in assessing phyletic changes in size. Specimens lumped together from all arenaceous facies exhibit an overall, albeit oscillatory, decrease in size from 90 mm (Aalenian) to 90 mm (L. Bajocian) to 71 mm (U. Bajocian) to 55 mm (U. Bathonian) to 55 mm (L. Callovian) to 80 mm (Oxfordian) to 57 mm (M. Tithonian) and this is corroborated, for at least part of the stratigraphic range, by a consistent reduction in size in condensed arenaceous facies from the Aalenian to the L. Bajocian to the L. Callovian (values as above). The reduced H/UA observed in some M. Tithonian specimens may not extend to other populations and so cannot definitely be considered as a phyletic effect, especially in the light of a plaubsible alternative explanation in terms of reduced growth rate (see Section 8).

Entolium (Entolium) orbiculare (J. Sowerby 1817)

Pl. 1, Fig. 19; text figs. 38–42

Synonymy

1817	*Pecten orbicularis* sp. nov; J. Sowerby, p. 193, pl. 86.
? 1829	*Pecten* sp; Phillips, pl. 5, fig. 11.
pv? 1836	*Pecten cingulatus* sp. nov; Goldfuss, p. 74, pl. 99, figs. 3a, 3b.
? 1837	*Pecten concentricus* sp. nov; Koch and Dunker, p. 43, pl. 5, fig. 8.
v*? 1840b	*Pecten partitus* sp. nov; J. de C. Sowerby, p. 328, pl. 22, figs. 5, 5a.
1843	*Pecten nummularis* sp. nov; G. Fischer, p. 135, pl. 5, fig. 4.
(?) *1850*	*Pecten partitus* J. de C. Sowerby, d'Orbigny, v. 1, p. 342.
1850	*Pecten nummularis* G. Fischer; d'Orbigny, v. 1, p. 373.

v non 1852 *Pecten cingulatus* GOLDFUSS; QUENSTEDT, p. 506, pl. 40, fig. 41.
non 1864 *Pecten concentricus* KOCH and DUNKER; V. SEEBACH, p. 100.
? 1866 *Pecten demissus* PHILLIPS; LINDSTROM, p. 14, pl. 3, figs. 9, 10 (non PHILLIPS sp.).
non 1869 *Pecten cingulatus* GOLDFUSS; TERQUEM and JOURDY, p. 127.
? 1874 *Pecten polylasmites* sp. nov; GEMMELLARO and DI BLASI, p. 137, pl. 3, fig. 18.
? 1876 *Pecten Pilatensis* sp. nov; FAVRE, p. 65, pl. 7, fig. 3.
? 1881 *Pecten vitreus* ROEMER; DE LORIOL, p. 93, pl. 13, figs. 3–5 (non ROEMER sp.).
? 1883 *Pecten demissus* PHILLIPS; LUNDGREN, p. 16, pl. 2, fig. 12 (non PHILLIPS sp.).
(?) 1885 *Pecten (Amusium) Pilatensis* FAVRE; NICOLIS and PARONA, p. 45.
non 1891 *Pecten concentricus* KOCH and DUNKER; BEHRENDSEN, p. 416.
? 1893 *Pecten (Entolium) theodosianus* sp. nov; RETOWSKI, p. 283, pl. 14, fig. 23.
1893 *Pecten (Entolium) erraticus* sp. nov; FIEBELKORN, p. 400, pl. 14, fig. 12.
non 1893 *Pecten (Entolium) cingulatus* GOLDFUSS; BOTTO-MICCA, p. 174.
? 1895 *Pecten Stewartianus* sp. nov; LUNDGREN, p. 198, pl. 3, fig. 12.
non 1898 *Pecten (Entolium) cingulatus* GOLDFUSS; GRECO, p. 109, pl. 8, figs. 30, 31.
1908 *Pecten (Entolium) gothicus* sp. nov; KRAUSE, p. 256, pl. 4, figs. 6, 7.
? 1910 *Pecten (Entolium) cingulatus* GOLDFUSS; RAVN, p. 464, pl. 33, fig. 7.
1910 *Pecten erraticus* FIEBELKORN; RAVN, p. 464.
? 1911 *Pecten (Entolium) cingulatus* GOLDFUSS; ROLLIER, p. 263.
? 1912 *Chlamys (Syncyclonema) Briconensis* COSSMANN; COSSMANN, p. 3, pl. 1, fig. 20.
? 1917 *Pecten vitreus* ROEMER, BORISSIAK and IVANOFF, p. 8, pl. 1, fig. 4 (non figs. 1, 2, 12, 16; non ROEMER sp.).
? 1923 *Syncyclonema masticonense* sp. nov: LISSAJOUS, p. 166, pl. 30, fig. 6.
? 1926 *Entolium cingulatum* (GOLDFUSS); STAESCHE, p. 93, pl. 4, figs. 3, 4.
? 1926 *Entolium* aff. *solido* (ROEMER); STAESCHE, p. 103, pl. 3, figs. 13–15 (non ROEMER sp.).
1931 *Pecten (Entolium) nummularis* G. FISCHER; SOKOLOV and BODYLEVSKY, p. 51, pl. 8, fig. 1.
non 1936 *Entolium cingulatus* (GOLDFUSS); DECHASEAUX, p. 60.
(?) 1936 *Entolium masticonense* (LISSAJOUS); DECHASEAUX, p. 63.
1936 *Entolium nummularis* (G. FISCHER); SPATH, p. 103, pl. 41, figs. 9, 10a–c, pl. 42, figs. 11a, 11b.
non 1951 *Entolium cingulatum* (GOLDFUSS); TROEDSSON, p. 217, pl. 20, figs. 1–3, pl. 21, figs. 11, 12.
? 1952 *Entolium partitum* (J. DE C. SOWERBY); COX, p. 35, pl. 3, figs. 11–13.
non *1961* *Entolium cingulatum* (GOLDFUSS); BARBULESCU, p. 702.
non 1964 *Entolium cingulatum* (GOLDFUSS); WELLNHOFER, p. 35, pl. 1, figs. 28–30.
? 1965 *Entolium briconense* (COSSMANN); COX, p. 51, pl. 6, fig. 6.
? 1965 *Entolium cingulatum* (GOLDFUSS); COX, p. 52, pl. 6, fig. 5.
1966 *Entolium nummulare* (G. FISCHER); ZAKHAROV, p. 35, pl. 5, fig. 3, pl. 6, figs. 2–6.
? *1970* *Entolium cingulatum* (GOLDFUSS); BEHMEL, p. 62.
1971 *Entolium (Entolium) orbiculare* (J. SOWERBY); DHONDT, p. 8, pl. 1, figs. 1a, 1b.
non *1971* *Entolium cingulatum* (GOLDFUSS); BARBULESCU, p. 277.
? *1971* *Entolium* cf. *cingulatum* (GOLDFUSS); WENDT, p. 160.
? 1972 *Entolium* sp. aff. *partitum* (J. DE C. SOWERBY); HAYAMI, p. 199, pl. 34, fig. 9.
1974 *Entolium nummulare* (G. FISCHER); ZAKHAROV and MESEZNIKOV, p. 140.
? *1974* *Entolium cingulatum* (GOLDFUSS); NITZOPOULOS, p. 46.
1977 *Entolium (Entolium) orbiculare* (J. SOWERBY); KELLY, p. 66, pl. 4, figs. 1–10.
? 1978 *Entolium* sp. A; DUFF, p. 64, pl. 5, figs. 7–10, 12, 13, 17.

The holotype (M) of *Pecten orbicularis* J. SOWERBY 1817, p. 193, pl. 86 has not been located in the SOWERBY Collection at the BM and is probably lost. It was derived from the U. Greensand (Albian) of Devizes, Wiltshire.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

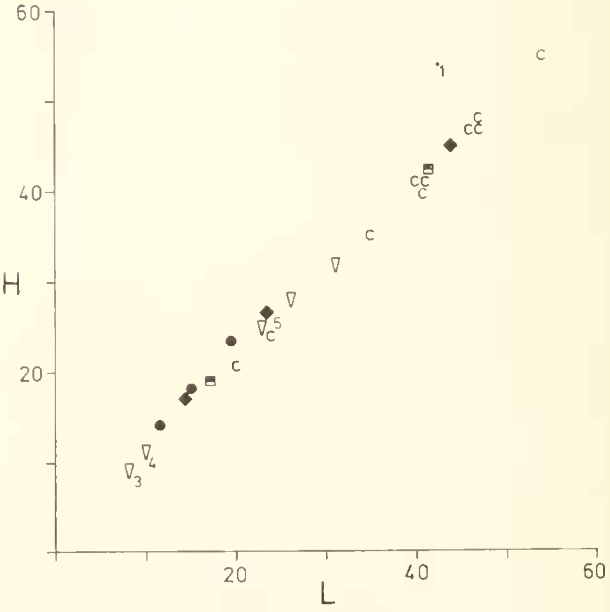
'Orbicular, much depressed, concentrically striated; striae elevated, sharp; one valve smooth; ears nearly equal, broadest at the base.

A thin tender shell; the striae are many, a line distant from each other; the length and breadth are equal; the ears rather large.

One of the tender products of the green sand of the Devizes canal, preserved by Mrs. GENT. It appears to be infrequent, as I have seen but one individual.'

2. AMENDED DIAGNOSIS

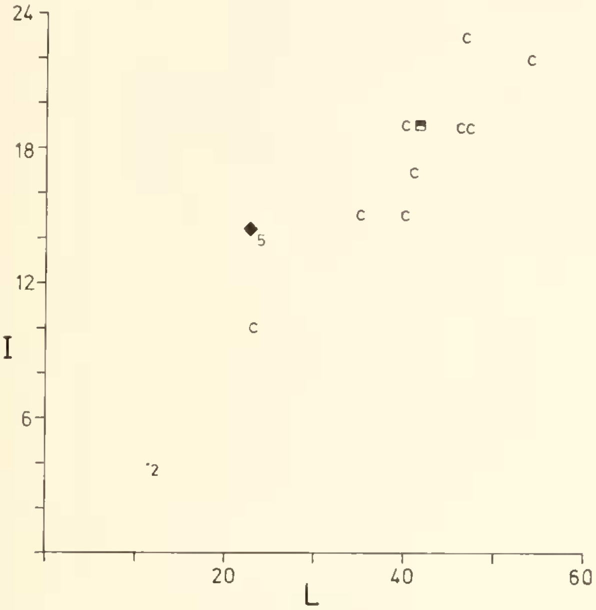
Distinguished from *E. (E.) corneolum* and *E. (E.) lunare* by the presence of regular comarginal grooves on the right valve.



Text fig. 38: *Entolium (E.) orbiculare* – height/length.

3. AMENDED DESCRIPTION

Essentially very similar to *E. (E.) corneolum*. Differing only by the diagnostic comarginal grooves (see Section 2) which are situated at intervals of between 1 and 4 mm (Kelly, 1977), by the smaller maximum height (54 mm; IGS R. 27/06) and by the somewhat lower mean H/L, H/UA and I/L (text figs. 38–40).



Text fig. 39: *Entolium (E.) orbiculare* – intersinal distance/length.

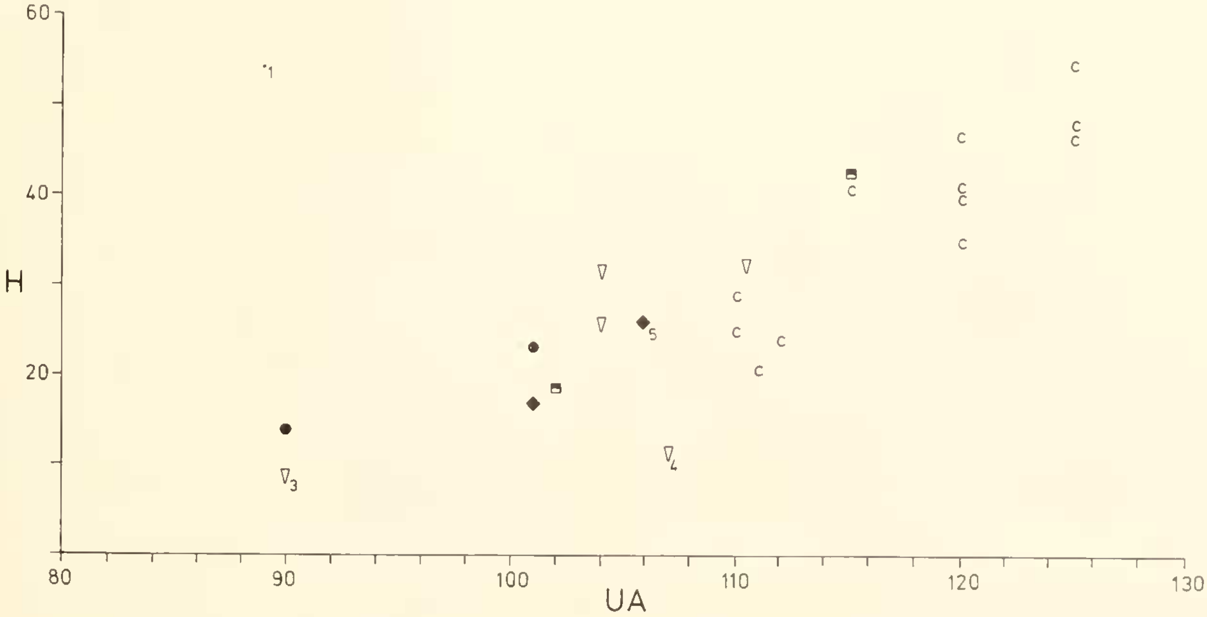
4. DISCUSSION

The earliest specific name erected for the species described in Section 3, *'Pecten' orbicularis* J. Sowerby, was founded on a Cretaceous specimen and most subsequent records of J. Sowerby's species have been from that period. For synonymy lists of Cretaceous *E. (E.) orbiculare* and synonymous species, reference should be made to Dhondt (1971) and Kelly (1977).

The figure of *'P.' nummularis* G. Fischer depicts a shell which lacks the comarginal grooves diagnostic of *E. (E.) orbiculare*. However, the description specifies such ornament thus the figure probably illustrates the smooth left valve of the latter species. Only Jurassic records of G. Fischer's species are included in the synonymy. Cretaceous records may be traced through Dhondt (1971) and Kelly (1977). It should be noted that some subsequent authors (e. g. d'Orbigny, 1850; Zakharov, 1966) have attributed *'P.' nummularis* incorrectly to Phillips while Sokolov and Bodylevsky (1931) have attributed the name to d'Orbigny.

The figure of *'P.' concentricus* Koch and Dunker, from the Kimmeridgian/Tithonian of N. Germany, depicts a specimen lacking a byssal notch and with strong comarginal ornament as in *E. (E.) orbiculare*. However, H/L and H/UA (1) are extremely high and although this could be due to bad drawing, the fact that v. Seebach (1864) and Behrendsen (1891), both of whom may well have examined the type material, have attributed specimens with radial ornament to *'P.' concentricus*, suggests that Koch and Dunker's figure is more probably of a left valve of *Camptonectes (Camptochlamys) obscurus*.

J. de C. Sowerby's (1840b) figures of *'P.' partitus* from the probable Callovian (Cox, 1952) of Cutch (India) reveal quite strong comarginal ornament, as in the right valve of *E. (E.) orbiculare*. However, the syntypes (BM R. 9960) do not exhibit such ornament and although one has I/L (2) within the range of *E. (E.) orbiculare* they are too poorly preserved to be specifically determinate. Cox (1952) has figured topotype specimens which show comarginal grooves similar in form to those of *E. (E.) orbiculare* but the apparent lack of smooth valves suggests that they comprise both right and left valves of a species which, unlike *E. (E.) orbiculare*, is comarginally ornamented on both valves (cf. *'Syncyclonema' masticonense*



Text fig. 40: *Entolium (E.) orbiculare* – height/umbonal angle.

below). Hayami's (1972) record of a form from the Toarcian of Vietnam having affinities with J. de C. Sowerby's species is based on a specimen which is too poorly preserved to be specifically determinate.

'P.' polylasmites Gemmellaro and di Blasi from the Tithonian of Sicily was founded on two specimens with regular comarginal ornament and no byssal notch. Both were said to be left valves but if this is the case the figure indicates that PH must be greater than AH, a situation unknown in other pectinids. It seems much more likely that the specimens are right valves which are thus very similar in ornament to the corresponding valve of *E. (E.) orbiculare.* Metric proportions (3) are indistinguishable.

'P.' (E.) theodosianus Retowski from the Tithonian of the Crimea is reported to be known only from left valves thus the strong comarginal ornament of the figured specimen cannot indicate any relationship with *E. (E.) orbiculare.* However, since Retowski states that a byssal notch is absent in his species right valves must have been available and it is thus possible that the comarginal ornament is limited to these specimens as in *E. (E.) orbiculare.* Nevertheless, H/UA (4) of the figure is somewhat low for the latter species.

'P.' (E.) erraticus Fiebelkorn and *'P.' (E.) gothicus* Krause from the German Kimmeridgian both have the comarginally grooved right valve of *E. (E.) orbiculare.* I/L (5) of the figure of the former is somewhat high but this could be due to inaccurate reproduction. H/L and H/UA are indistinguishable from *E. (E.) orbiculare.*

The figure of *'Chlamys' ('Syncyclonema') Briconensis* Cossmann; Cossmann (1912) from the Callovian of France reveals strong comarginal ornament, as in the right valve of *E. (E.) orbiculare,* but the description specifies unequal auricles, which may serve to differentiate the species. Unfortunately the degree of auricle asymmetry cannot be assessed because of the poor preservation of the figured specimen. Cox's (1965) record of Cossmann's species from the same horizon in E. Africa is based on a similarly poorly preserved specimen. Cossmann's original description and figure (1907c) has proved impossible to trace. The auricles of *'S.' masticonense* Lissajous, a species from the U. Bajocian and L. Bathonian of France which was compared with Cossmann's species, are somewhat better preserved and seem to be entolioid in form. The comarginal ornament of the right valve is indistinguishable from that of *E. (E.) orbiculare* but that of the left valve, said to consist of lamellose comarginal striae, may serve to differentiate the species.

The questionably synonymous species *'P.' cingulatus* Goldfuss (and secondary references thereto) is discussed under *E. (E.) corneolum.*

The remaining questionable references listed in synonymy are discussed under *E. (E.) corneolum* (for Favre, 1876; de Loriol, 1881; Staesche, 1926) and *E. (E.) lunare* (for Phillips, 1829; Lindstrom, 1866; Lundgren, 1883, 1895; Borissiak and Ivanoff, 1917; Duff, 1978).

5. STRATIGRAPHIC RANGE

Kelly (1977) states that specimens from the Kimmeridgian (e. g. IGS Y1624, Y1625; GPIG; MNR; Fiebelkorn, 1893; Krause, 1908; Sokolov and Bodylevsky, 1931; Zakharov, 1966, 1974) constitute the earliest records of *E. (E.) orbiculare.* In fact, Sokolov and Bodylevsky (1931) record the species from the Oxfordian of Spitzbergen, d'Orbigny (1850) records it from the Oxfordian of various localities in France and Russia and univalved comarginally grooved museum specimens from the same stage in England (BM L66462), Germany (GPIG) and France (MNS) probably constitute further records of the species. Bibliographic records in Phillips (1829), Favre (1866), Nicolis and Parona (1885), Rollier (1911), Staesche (1926), Behmel (1970), Wendt (1971) and Nitzopoulos (1974) may also refer to Oxfordian examples of *E. (E.) orbiculare* (see Section 4). Earlier records (in the Callovian: J. de C. Sowerby, 1840; d'Orbigny, 1850; Cossmann, 1912; Cox, 1952, 1965; Duff, 1978; in the Bajocian and Bathonian: Lissajous, 1923; Dechaseaux, 1936; in the Toarcian: Hayami, 1972) are restricted to questionably

Text fig. 41: *Entolium (E.) orbiculare* – European distribution.

Text fig. 42: *Entolium (E.) orbiculare* – World distribution (Tithonian reconstruction).

synonymous species and until pre-Oxfordian bivalved specimens with smooth left valves and comarginally ornamented right valves are discovered it is probably best to say that the first appearance of *E. (E.) orbiculare* is in the U. Jurassic. It is possible that another species with comarginal grooves on both valves may have existed in the M. Jurassic (see Section 4).

In the Oxfordian and Kimmeridgian *E. (E.) orbiculare* is only known to be common in Spitzbergen (Sokolov and Bodylevsky, 1931). Subsequently in the Jurassic it is not known to be common anywhere. Kelly (1977) reports the species as abundant in the M. Volgian (≃ M. Tithonian) to Ryazanian (Cretaceous) of E. England and Dhondt (1971) states that *E. (E.) orbiculare* is known until the Turonian.

6. GEOGRAPHIC RANGE

The distribution of *E. (E.) orbiculare* in the Jurassic is distinctly Boreal with no certain records south of a palaeolatitude of about 25°N (text figs. 41, 42).

7. DESCRIPTION OF ECOLOGY

In Spitzbergen, Sokolov and Bodylevsky (1931) record common *E. (E.) orbiculare* in association with *E. (E.) corneolum* in U. Oxfordian to L. Kimmeridgian black shales. In E. Greenland Spath (1936) records *E. (E.) orbiculare* with a height of 42.5 mm from U. Tithonian ('Portlandian') glauconite sands and similar sediments are probably the source of a number of specimens from the L. Volgian (≃ L. Tithonian) of the Moscow area where *E. (E.) corneolum* also occurs. According to Kelly (1977) the same sedimentary facies is dominated by *E. (E.) orbiculare* in the Spilsby and Sandringham Sands (M. Volgian to Ryazanian) of E. England. Current aligned specimens in the stable, convex up, position constitute between 51 and 57% of the total fauna. In the remainder, the deep burrowing bivalves *Pleuromya* and *Pholadomya* are quite common elements. In finer grained sands whose fauna contains a higher proportion of byssate and cemented bivalves indicating deposition under lower energy conditions, *E. (E.) orbiculare* constitutes only 28% of the total fauna. The maximum height attained in the sequence is 55 mm (IGS R27/06).

8. INTERPRETATION OF ECOLOGY

The variations in abundance of *E. (E.) orbiculare* in the Spilsby and Sandringham Sands suggest that the species favoured high energy environments. However, the relatively greater abundance in coarse, high energy sands could merely be due to post-mortem winnowing out of small elements of the fauna to leave concentrations of *E. (E.) orbiculare* in such sediments. By adopting a view that the species was, in fact, eurytopic with respect to environmental energy the otherwise anomalous occurrence of *E. (E.) orbiculare* in black shales in Spitzbergen is reasonably explained.

There is no evidence of any competitive reaction between *E. (E.) orbiculare* and *E. (E.) corneolum.*

9. FUNCTIONAL MORPHOLOGY

Since *E. (E.) orbiculare* is in all important aspects of morphology identical to *E. (E.) corneolum* a similar reclining/swimming mode of life can be inferred. The development of pronounced comarginal ornament on the right valve exterior represents, at least in the high energy environments occupied by the species (see Section 8), an improved adaptation for reclining since it increases purchase on the substrate and thereby promotes stability.

10. ORIGINS AND EVOLUTION

The most obvious ancestor for *E. (E.) orbiculare* is *E. (E.) corneolum*. However, it should be borne in mind that a second species, morphologically very similar to *E. (E.) orbiculare*, may have existed in the M. Jurassic (see Section 4) and been a more direct ancestor of *E. (E.) orbiculare*. Except for H/L, the slight differences in the metric proportions of *E. (E.) orbiculare* in comparison with *E. (E.) corneolum* (see Section 3) cannot be explained by heterochrony as the latter species displays little allometry in the relevant features.

The available data on maximum height (42.5 mm: 'Portlandian', 54 mm: M. Volgian-Ryazanian) is not sufficiently localised in a stratigraphic sense to allow any assessment of possible phyletic changes.

Genus *PSEUDOPECTEN* Bayle 1878

Type species. M; Bayle 1878, pl. 21, fig. 1; *Pecten equivalvis* J. Sowerby 1816, p. 83, pl. 136, fig. 1; U. Pliensbachian, Avallon, E. Paris Basin.

AMENDED DIAGNOSIS

Nearly equivalve to clearly inequivalve; between 12 and 27 radial plicae which are nearly smooth or with spines on RV. L. Jur.–M. Jur., Eu., N. and S. Am., E. Indies.

DISCUSSION

In his diagnosis Hertlein (1969: N372) stated that *Pseudopecten* was nearly equivalve; *Ps. (Echinopecten) barbatus* is, however, distinctly inequivalve. Hertlein stated that about 15 or 16 plicae were present; text fig. 43 shows that there is at least a range between 12 and 27 plicae. Hertlein excluded N. America from the geographic range; the latter continent can now be included on the basis of the results of work presented herein.

Subgenus *PSEUDOPECTEN* s. s.

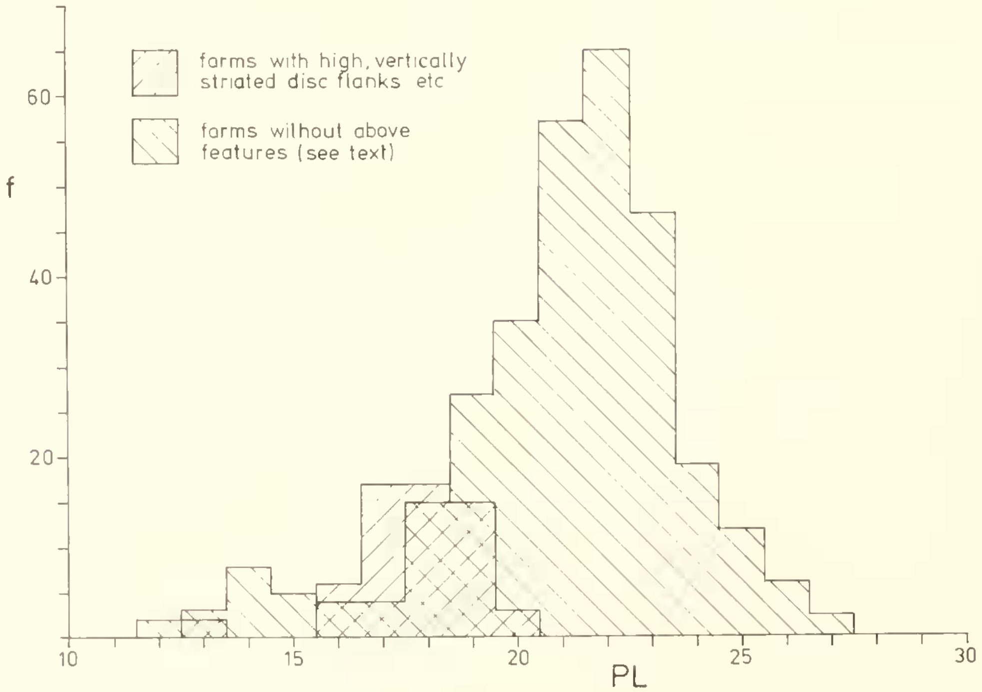
AMENDED DIAGNOSIS

Plicae on right valve smooth or some with spines; nearly equivalve. L. Jur.–M. Jur. (Hettang.–Bajoc.), Eu., N. Afr., N. and S. Am.

DISCUSSION

Hertlein (1969: N372) omitted any reference to convexity in his diagnosis, which consequently does not exclude *Ps. (Echinopecten)*. He erroneously limited the stratigraphic range to Sinemurian – Domerian and the geographic range to Europe.

Within *Ps. (Pseudopecten)* two groups may be distinguished by the presence or absence of high, vertically striated disc flanks and comarginal striae which tongue down the sulci. Forms possessing these features usually have between 16 and 20 plicae (text fig. 43). However 2 specimens with 13 plicae are known to possess these features and it seems extremely likely that forms with between 12 and 15 plicae, most of which are poorly preserved, also possessed them originally. This group has a bimodal plical frequency distribution with peaks at 14 and 17/18 plicae. Such a distribution is herein considered to be indicative of two species named, respectively, *Ps. (Ps.) veyrasensis* and *Ps. (Ps.) dentatus*. However, the possibility cannot be entirely discounted that it is indicative of a single polymorphic species. Apart from the number of plicae, forms with between 12 and 15 plicae are virtually indistinguishable from those with between 16 and 20 plicae. However, in spite of close ecological similarities the two groups are not congruent stratigraphically (see pp. 79, 75) and this is most easily interpreted as the result of a specific difference in the absence of more positive proof for polymorphism.



Text fig. 43: *Pseudopecten (Pseudopecten)* – frequency distribution for number of plicae.

Forms without high, vertically striated disc flanks and comarginal striae which tongue down the sulci have between 16 and 27 plicae (mode 22) and are herein referred to *Ps. (Ps.) equivalvis*. Differences in size, umbonal angle and angularity of the plicae in forms referred to this species can be confidently ascribed to ontogenetic and ecophenotypic variation (see pp. 64, 71).

Pseudopecten (Pseudopecten) equivalvis (J. Sowerby 1816)

Pl. 2, Figs. 1, 2, 4–10, ?Fig. 3; text figs. 44–58

Synonymy

v 1816 *Pecten equivalvis* sp. nov; J. Sowerby, p. 83, pl. 136, fig. 1.
1819 *Pecten acuticosta* sp. nov; Lamarck, p. 180.
? 1820 *Pectinites priscus* sp. nov; Schlotheim, p. 222.
1828 *Pecten sublaevis* sp. nov; Young and Bird, p. 234, pl. 9, figs. 9, 10.
1828 *Pecten major* sp. nov; Young and Bird, p. 235.
1833 *Pecten acuticostatus* Lamarck; v. Zieten, p. 70, pl. 53, figs. 6a, 6b.
1833 *Pecten aequivalvis* J. Sowerby; v. Zieten, p. 68, pl. 52, figs. 4a, 4b.
1833 *Pecten costatulus* sp. nov; Hartmann in v. Zieten, p. 68, pl. 52, figs. 3a, 3b.
v 1833 *Pecten aequivalvis* J. Sowerby; Goldfuss, p. 43, pl. 89, fig. 4.
v non 1833 *Pecten priscus* Schlotheim; Goldfuss, p. 43, pl. 89, fig. 5.
v 1833 *Pecten acutiradiatus* sp. nov; Münster in Goldfuss, p. 44, pl. 89, figs. 6a–c.
1836 *Pecten aequivalvis* J. Sowerby; Roemer, p. 67.
1836 *Pecten acuticosta* sp. nov; Roemer, p. 68.
? 1838 *Pecten lugdunensis* sp. nov; Michelin in Leymerie, pl. 24, fig. 5.
v *1850* *Pecten aequivalvis* J. Sowerby; d'Orbigny, v. 1, p. 237.
v *1850* *Pecten priscus* Schlotheim; d'Orbigny, v. 1, p. 238.
v *1850* *Pecten cephus* sp. nov; d'Orbigny, v. 1, p. 238.
v 1850 *Pecten acuticosta* Lamarck; d'Orbigny, v. 1, p. 257.
1850 *Pecten acutiradiatus* Münster; d'Orbigny, v. 1, p. 257.
1851 *Pecten acutiradiatus* Münster; Schafhautl, p. 410.
1852 *Pecten acuticosta* Lamarck; Verneuil and Collomb, p. 112.
1852 *Pecten aequivalvis* J. Sowerby; Bronn, p. 208, pl. 19, fig. 4.
1852 *Pecten priscus* Schlotheim; Quenstedt, p. 507, pl. 40, fig. 42.
1853 *Pecten acuticosta* Lamarck; Chapuis and Dewalque, p. 211, pl. 31, figs. 3a–c.
1853 *Pecten aequivalvis* J. Sowerby; Chapuis and Dewalque, p. 212, pl. 32, fig. 1.
1853 *Pecten aequivalvis* J. Sowerby; Oppel, p. 77, pl. 4, fig. 11.
1853 *Pecten priscus* Schlotheim; Oppel, p. 78, pl. 4, fig. 10.
1858 *Pecten aequivalvis* J. Sowerby; Oppel, p. 181.
1858 *Pecten sublaevis* Young and Bird; Oppel, p. 181.
1858 *Pecten priscus* Schlotheim; Oppel, p. 181.
v 1858 *Pecten aequalis* sp. nov; Quenstedt, p. 78, pl. 9, fig. 13.
1858 *Pecten aequivalvis* J. Sowerby; Quenstedt, p. 183, pl. 23, fig. 1.
1860 *Pecten aequivalvis* J. Sowerby; Coquand, p. 62.
1863 *Pecten priscus* Schlotheim; Schlönbach, p. 542.
1865 *Pecten aequalis* Quenstedt; Terquem and Piette, p. 102, pl. 12, figs. 15–19.
1867 *Pecten acutiradiatus* Münster; Dumortier, pp. 72, 217, pl. 48, figs. 5, 6.
non 1867 *Pecten priscus* Schlotheim; Dumortier, p. 216, pl. 48, fig. 4.
1869 *Pecten acutiradiatus* Münster; Dumortier, p. 135, pl. 21, fig. 8.
1869 *Pecten acuticostatus* Lamarck; Dumortier, p. 136, pl. 21, fig. 7, p. 305, pl. 39, fig. 3.
1869 *Pecten priscus* Schlotheim; Dumortier, p. 138, pl. 22, fig. 3.
1869 *Pecten aequivalvis* J. Sowerby; Dumortier, p. 298, pl. 42, figs. 16, 17.
1871 *Pecten priscus* Schlotheim; Brauns, p. 390.
1871 *Pecten aequivalvis* J. Sowerby; Brauns, p. 391.
1872 *Pecten aequivalvis* J. Sowerby; Tietze, p. 106.
1872 *Pecten Hinterhuberi* sp. nov; Tietze, p. 107, pl. 3, fig. 4.
1876 *Pecten aequalis* Quenstedt; Tate and Blake, p. 363.
1876 *Pecten aequivalvis* J. Sowerby; Tate and Blake, p. 363.
1876 *Pecten priscus* Schlotheim; Tate and Blake, p. 364.
1878 *Pseudopecten aequivalvis* (J. Sowerby); Bayle, pl. 121, fig. 1.
1881 *Pecten Caracolensis* sp. nov; Steinmann, p. 254, pl. 14, fig. 10.
1884 *Pecten acuticostatus* Lamarck; Uhlig, p. 179.
1884 *Pecten* cf. *aequivalvis* J. Sowerby; Uhlig, p. 179.
1884 *Pecten major* Young and Bird; Simpson, p. 165.
1884 *Pecten sublaevis* Young and Bird; Simpson, p. 165.
1884 *Pecten interstinctus* sp. nov; Simpson, p. 169.
1884 *Pecten rudis* sp. nov; Simpson, p. 169.
1884 *Pecten dichotomus* sp. nov; Simpson, p. 169.
1886 *Pecten aequivalvis* J. Sowerby; Winkler, p. 30.
1888 *Pecten priscus* Schlotheim; Moberg, p. 34, pl. 1, fig. 26.
? 1890 *Pecten Norigliensis* sp. nov; Tausch, p. 13, pl. 7, fig. 8.
? 1891 *Pecten Bodenbenderi* sp. nov; Behrendsen, p. 391, pl. 22, fig. 3.
? 1895 *Pecten Johnstrupi* sp. nov; Lundgren, p. 199, pl. 3, figs. 13a, 13b.
1897 *Pecten priscus* Schlotheim; Pompeckj, pp. 773, 776.
1897 *Pecten aequivalvis* J. Sowerby; Pompeckj, pp. 776, 779.
1897 *Pecten acuticosta* Lamarck; Pompeckj, p. 776.
1903 *Pecten aequalis* Quenstedt; Bistram, p. 37, pl. 3, figs. 4, 5.
1909 *Pecten (Chlamys) priscus* Schlotheim; Trauth, p. 92.
1910 *Chlamys aequivalvis* (J. Sowerby); Lissajous, p. 352, pl. 10, fig. 2.
1916 *Pecten priscus* Schlotheim; Jaworski, p. 417.
1916 *Chlamys (Aequipecten) prisca* (Schlotheim); Cossmann, p. 47, pl. 5, fig. 16.
? 1920 *Pecten zigoplocus* Di Blasi; Fucini, p. 89, pl. 5, figs. 13, 14.
1924 *Chlamys mcconnelli* sp. nov; McLearn, p. 46, pl. 5, figs. 1, 9.
1925 *Pecten acutiradiatus* Münster; Dubar, p. 259.
1925 *Pecten acuticosta* Lamarck; Dubar, pp. 275, 282.
1925 *Pseudopecten aequivalvis* (J. Sowerby); Dubar, p. 277.
1926 *Aequipecten priscus* (Schlotheim); Staesche, p. 48.
1926 *Aequipecten acuticosta* (Lamarck); Staesche, p. 50, pl. 6, figs. 1, 2.

1926 *Aequipecten aequivalvis* (J. Sowerby); Staesche, p. 51.
1926 *Chlamys aequivalvis* (J. Sowerby); Roman, p. 113.
1929 *Pecten (Pseudopecten) acuticosta* Lamarck; Lanquine, p. 130.
1929 *Pecten (Pseudopecten) priscus* Schlotheim; Lanquine, p. 131.
1932 *Pecten (Aequipecten) aequivalvis* J. Sowerby; Tzankov and Boncev, p. 231.
1935 *Chlamys sendelbachensis* sp. nov; Kühn, p. 470, pl. 18, fig. 32.
1936 *Aequipecten priscus* (Schlotheim); Kühn, p. 248, pl. 9, fig. 6.
1936 *Aequipecten acuticosta* (Lamarck); Kühn, p. 248, pl. 12, fig. 46.
1936 *Aequipecten aequivalvis* (J. Sowerby); Kühn, p. 248, pl. 10, fig. 19, pl. 13, fig. 24.
1936 *Aequipecten maximiliani* sp. nov; Kühn, p. 249, pl. 11, figs. 3a, 3b.
1936 *Pseudopecten acuticosta* (Lamarck); Dechaseaux, p. 59.
1936 *Pseudopecten aequivalvis* (J. Sowerby); Dechaseaux, p. 59.
1936 *Aequipecten priscus* (Schlotheim); Dechaseaux, p. 42.
1936 *Aequipecten acutiradiatus* (Münster); Dechaseaux, p. 42.
1942 *Aequipecten bierringi* sp. nov; Rosenkrantz, p. 26.
non 1948 *Pecten (Aequipecten) noriglensis* Tausch; Dubar, p. 163, pl. 13, fig. 12.
1951 *Pecten aequivalvis* J. Sowerby; Troedsson, p. 219.
1965 *Pecten priscus* Schlotheim; Dahm, pp. 27–29.
1965 *Pecten* cf. *acutiradiatus* Münster; Dahm, p. 27.
1965 *Pseudopecten aequivalvis* (J. Sowerby); Dahm, p. 28.
1965 *Chlamys acuticostata* (Lamarck); Mensink, p. 77.
1965 *Pecten aequivalvis* J. Sowerby; Mensink, p. 78.
1966 *Aequipecten priscus* (Schlotheim); Behmel and Geyer, p. 28.
1966a *Pseudopecten prisca* (Schlotheim); C. Palmer, p. 67.
1966b *Pseudopecten equivalvis* (J. Sowerby); C. Palmer, p. 72.
1966b *Pseudopecten prisca* (Schlotheim); C. Palmer, p. 72.
1967 *Pseudopecten priscus* (Schlotheim); Berridge and Ivimey-Cook, p. 160.
1972 *Pseudopecten aequivalvis* (J. Sowerby); Hallam, p. 408.

Lectotype of *Pecten equivalvis* J. Sowerby 1816, p. 83, pl. 136, fig. 1 designated herein; BM L79783; Pl. 2, Fig. 1 herein; H: 79, L: 85, I_L: 48, UA: 128; M. Lias (U. Pliensbachian), Ilminster, Somerset.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

'Lenticular with rounded diverging ribs and many acute concentric striae; valves equally convex the lower one smoothest; ears equal.

The ribs vary in proportion; they sometimes equal the space between them, but are generally less; they are rounded and the striae are more or less obliterated over them: the spaces between them are slightly concave.

Pectens are generically described by Lamarck as inequivalve, wherefore, I suppose, he had not seen any otherwise; but the present species has both valves nearly if not quite, equally gibbous; one valve being simply convex, the other having a trifling reversed undulation near the edge, and differing but little in the pattern. The auricles have not, as I have seen, been found perfect, they are, however, nearly so, and they then show an horizontal line on each side of the beak, with nearly perpendicular lineae or striae. I have one by favour of Dr. Sutton, which has nearly parallel lines with the hinge on the dexter auricle of the broader valve, with the broad costae. This species is commonly found from three to seven inches in diameter. Mr. Strangeways, from whom I have received several specimens, observes that they are characteristic of the coarse limestone of Ilminster. I have had other specimens from near Lackington, by favour of Mr. Strangeways, also from Farley gateway, Gloucestershire; Carrington, Oxfordshire; and from Dursley, Gloucestershire. I believe the species is found in various other parts of England, and I have a specimen from France.'

2. AMENDED DIAGNOSIS

Distinguished from *Ps. (Ps.) dentatus* and *Ps. (Ps.) veyrasensis* by the low disc flanks and curvilinear comarginal striae.

3. AMENDED DESCRIPTION

Disc sub-ovate, higher than long in juvenile, growing allometrically to become longer than high (text fig. 44) towards maximum height of 179 mm (BM 2662). Umbonal angle increasing at a decreasing rate (text fig. 45) to produce concave dorsal margins. Disc flanks low.

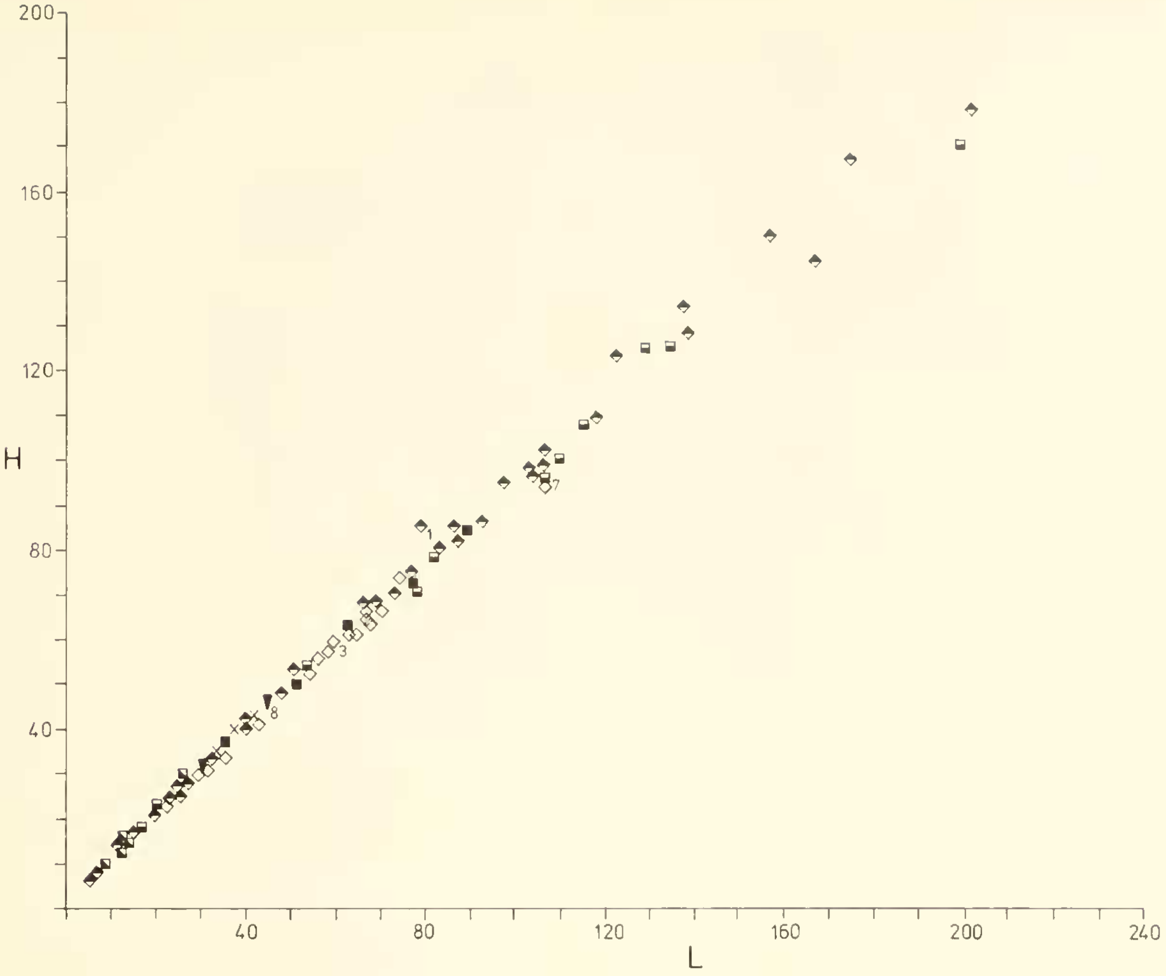
Equilateral, moderately convex, left valve slightly more convex than right.

Intersinal distance greater in left valve than right but increasing at a slightly increasing rate in both valves (text figs. 46, 47). Large byssal notch in right valve becoming relatively smaller during ontogeny (text fig. 48).

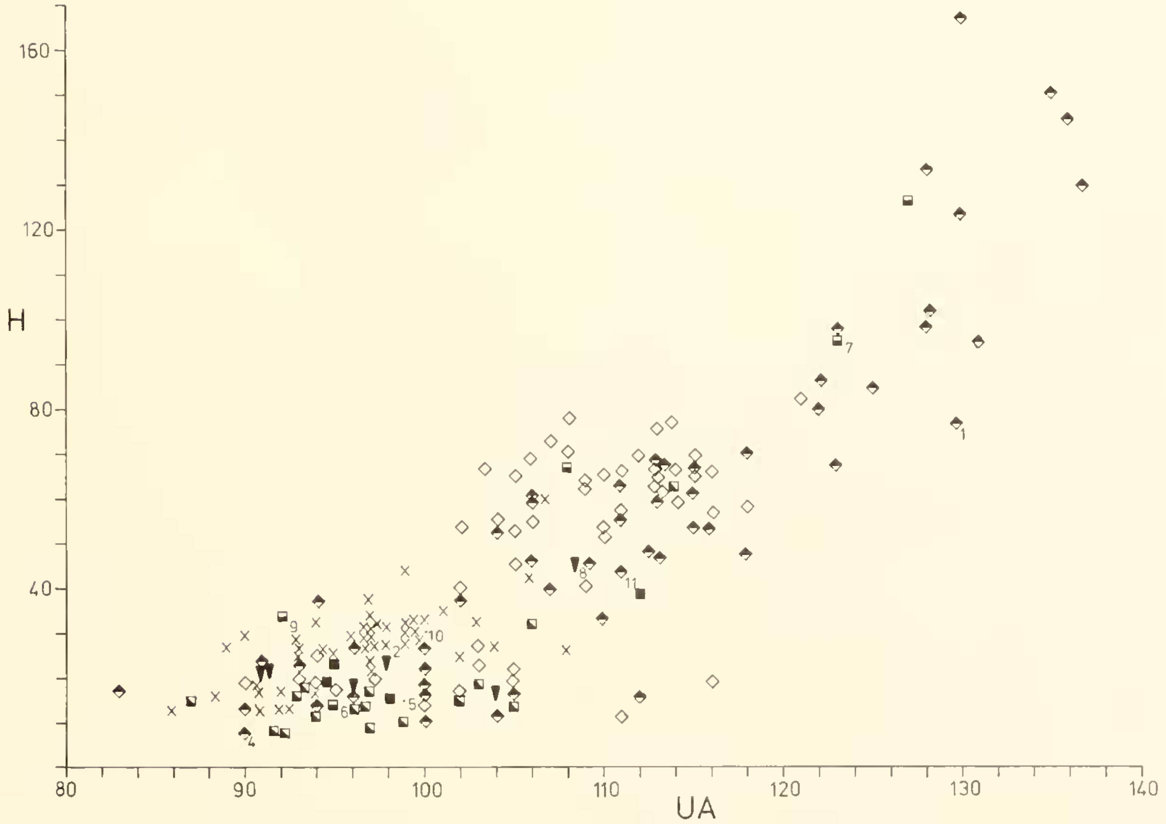
Auricles well demarcated from disc, moderate in size, anterior slightly larger than posterior. Both anterior and posterior hinge lengths increasing at an increasing rate (text figs. 50, 51). Anterior auricle height increasing at a decreasing rate (text fig. 49). All auricles meeting hinge line at approximately 90°. Anterior auricle of right valve meeting disc at approximately 90°, other auricles meeting disc at an acute angle. All auricles ornamented with comarginal striae, anterior auricles also bearing 2–3 fine radial costae.

Both valves ornamented with between 16 and 27, most commonly 22, radial plicae (text fig. 52). Plicae angular and often wider than sulci in juveniles but becoming more rounded and narrower than sulci later in ontogeny (Pl. 1, Fig. 8). Plicae poorly defined at anterior dorsal and posterior dorsal margins of juveniles. Both plicae and sulci bearing fine radial striae and crossed by closely spaced curvilinear comarginal striae.

Shell thickness generally moderate but high beneath plicae.



Text fig. 44: *Pseudopecten (Ps.) equivalvis* – height/length.



Text fig. 45: *Pseudopecten (Ps.) equivalvis* – height/umbonal angle.

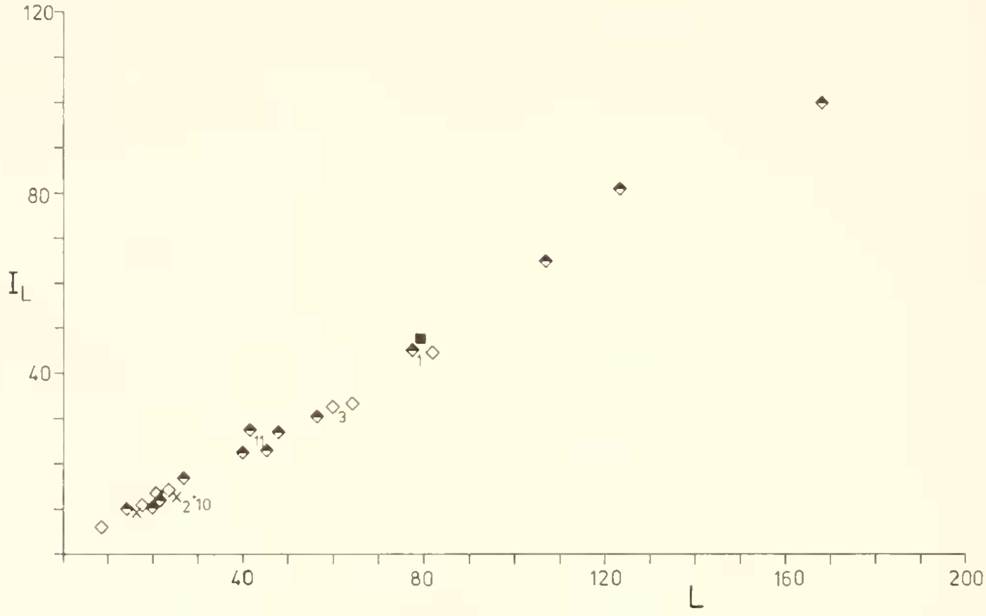
4. DISCUSSION

'Pecten' acuticosta LAMARCK only differs from *'P.' equivalvis* SOWERBY (lectotype [herein designated]; BM L79783; Pl. 2, Fig. 1; 1) by the angularity of the plicae. There can be little doubt that this is the result of a lower degree of abrasion (see Section 8) and it cannot therefore be the basis for a specific distinction. Most large specimens with angular plicae which are referred to *'P.' acuticosta* are derived from low energy condensed deposits and also have relatively low umbonal angles for their heights. However, this appears to be an ecophenotypic feature brought about by relatively fast growth in such facies (see Section 8).

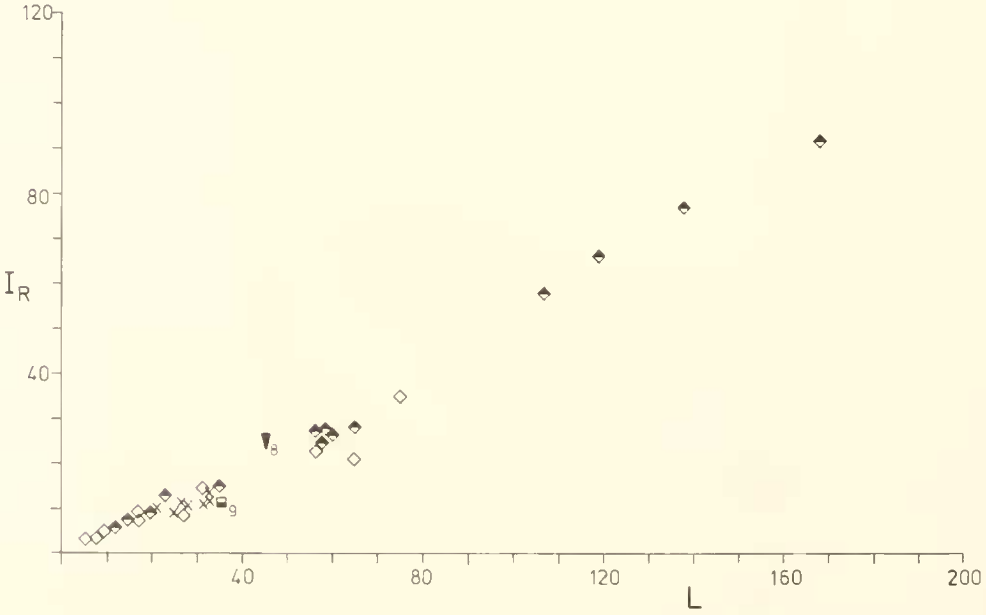
'Pectinites' priscus SCHLOTHEIM was erected for a single specimen from the Sinemurian exhibiting few diagnostic features. Subsequent authors have frequently applied the specific name to small specimens of *Ps. (Pseudopecten)* and have maintained a specific distinction from larger specimens (= *'P.' aequivalvis* auctt.) on the basis of a lower umbonal angle and reduced number of plicae, which tend also to be acute. Notwithstanding the fact that the holotype (M) of *'Pt.' priscus* (HM) is reported to be an abnormally large specimen (H: 80, Dr. J. HELMS, pers. comm., 1977) for its stratigraphic horizon, three further criteria indicate that *'P.' priscus* auctt. should be included within *Ps. (Ps.) equivalvis.*

a. Umbonal angle and the number of fully developed plicae both increase during ontogeny (see Section 3) thus small immature specimens of *Ps. (Ps.) equivalvis* have low umbonal angles and appear to have few plicae.

b. Mature specimens from argillaceous facies may exhibit the above characteristics because they are small as a result of stunting (see Section 8).



Text fig. 46: *Pseudopecten (Ps.) equivalvis* – intersinal distance on left valve/length.



Text fig. 47: *Pseudopecten (Ps.) equivalvis* – intersinal distance on right valve/length.

c. Mature specimens from low horizons in the stratigraphic range of *Ps. (Ps.) equivalvis* may exhibit the above characteristics because they are small as a consequence of representing an early stage in phyletic evolution towards increased maximum size (see Section 10).

It is very doubtful whether any of the records of *'P.' priscus* cited in synonymy represent anything other than one of the above categories of small *Ps. (Ps.) equivalvis.*

'P.' sublaevis Young and Bird was separated from *'P.' equivalvis* on the basis of its low plicae, lacking in comarginal striae. As discussed above, this is almost certainly due to abrasion. *'P.' major* Young and Bird appears to represent, by contrast, an unusually well preserved specimen of *Ps. (Ps.) equivalvis* which still exhibits radial striae on the plicae.

Simpson's (1884) species *'P.' interstinctus*, *'P.' rudis* and *'P.' dichtomus* were all compared with *'P.' priscus* and although figures were not provided it seems highly likely that the species represent small specimens of *Ps. (Ps.) equivalvis.*

The single observed type of *'P.' aequalis* Quenstedt (GPIT 4-9-13; Pl. 2. Fig. 5) has 22 plicae and is inseparable from *Ps. (Ps.) equivalvis* by metric criteria (2). Likewise, one of the syntypes of *'P.' cephus* d'Orbigny (MNO 1842C) has 17 plicae and is inseparable by metric criteria (3) while another (Pl. 2, Fig. 10) has 21 plicae and exhibits no distinguishing features.

Kühn's (1935) holotype (M) for *'Chlamys' sendelbachensis* (BSPHG 1934 IV 8; Pl. 2, Fig. 4) has 20 plicae and metric proportions (4) within the range of *Ps. (Ps.) equivalvis.* His type material for *'Aequipecten' maximiliani* appears to be lost but the diagnostic criteria, three more plicae than is usual in *Ps. (Ps.) equivalvis* (22) and reduced plical height, can both be accommodated within the known range of 'genetic' and 'environmental' variation in the latter species.

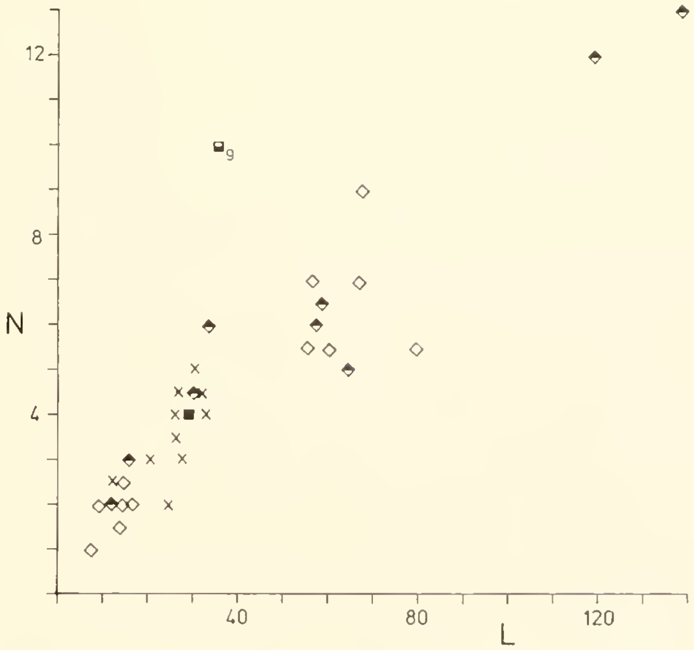
The figure of *'P.' costatulus* Hartmann exhibits 17–18 plicae and H/UA (5) which is indistinguishable from *Ps. (Ps.) equivalvis.* Similarly *'Ch.' mcconnelli* McLearn has 22 plicae and the description gives no grounds for considering the species as anything other than synonymous with *Ps. (Ps.) equivalvis.*

Münster's (1833) figure of *'P.' acutiradiatus* shows a specimen with an exceptionally large umbonal angle (125 at H: 13.5) and small auricles. However, examination of the figured specimen (BSPHG AS VII 611; Pl. 2, Fig. 9) shows this to be due to a draughting error. The auricles are in fact broken and the H/UA ratio (6) is well within the range of *Ps. (Ps.) equivalvis.*

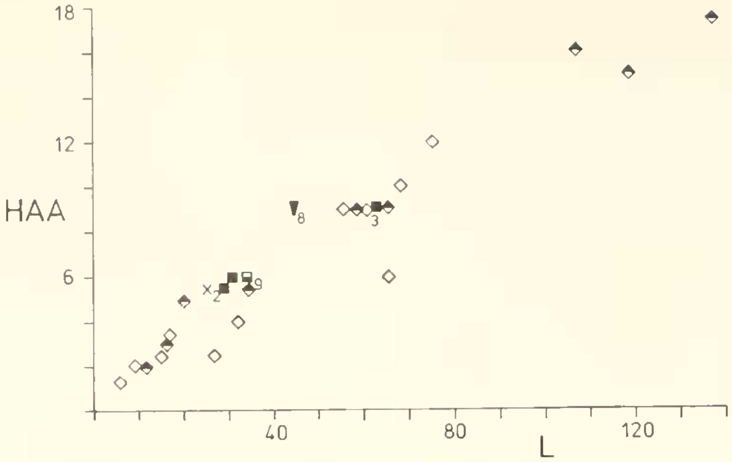
'P.' Hinterhuberi Tietze was erected for a very large specimen (H: 152) said to differ from *'P.' equivalvis* by its smaller umbonal angle. However, the figure depicts a broken specimen which could not have provided an accurate value for UA. In all other respects it is identical to *Ps. (Ps.) equivalvis.* The specimen was derived from a loose boulder thus the reported age (Hettangian, Angulata zone) may well be inaccurate. The apparently abnormal size for the stratigraphic horizon (see Section 10) may therefore be spurious.

'P.' Caracolensis Steinmann was erected for a specimen possessing 24 smooth low plicae and characterised by one large median plica. This last feature is fairly common in *Ps. (Ps.) equivalvis* and is probably caused by the interruption of normal growth by damage. The species are inseparable by metric criteria (7).

The figure of *'P.' lugdunensis* Michelin reveals a specimen with 25 plicae and metric proportions (8) which are inseparable from *Ps. (Ps.) equivalvis.* The four auricular costae may however be distinctive and subsequent authors who may have examined the type material (e. g. Staesche, 1926) have synonymised Michelin's species with *Ch. (Ch.) valoniensis* (q. v.). The preservation of *'P.' lugdunensis* as an internal mould may preclude recognition of the intercalary costae characteristic of *Ch. (Ch.) valoniensis.*



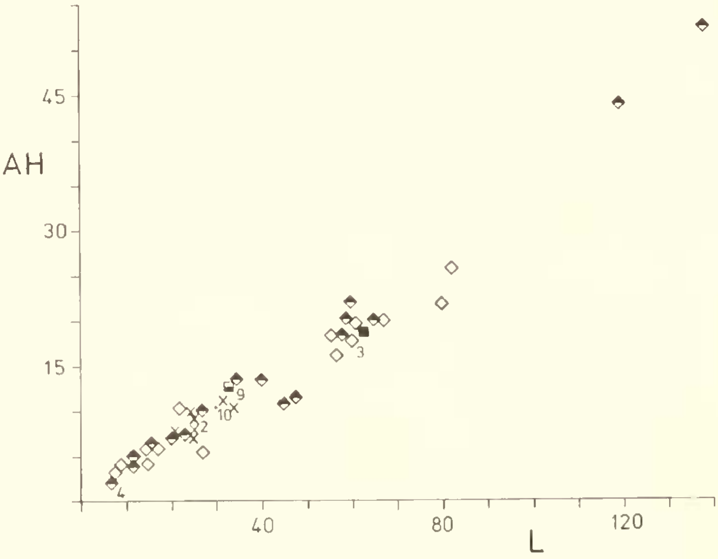
Text fig. 48: *Pseudopecten (Ps.) equivalvis* – depth of byssal notch/length.



Text fig. 49: *Pseudopecten (Ps.) equivalvis* - height of anterior auricle/length.

The figure of *'P.' Norigliensis* TAUSCH depicts a specimen with 19 plicae and H/UA, I_R/L and AH/L (9) just within the range of *Ps. (Ps.) equivalvis.* PH/L and, in particular, N/L are distinctly high. However, this could simply be due to inaccurate illustration and the single specimen recorded provides few grounds for a specific separation. DUBAR (1948), who may have examined the holotype (M), has applied TAUSCH's specific name to forms which are clearly conspecific with *Ps. (Ps.) dentatus* (q. v.).

The description and figures of *'P.' Bodenbenderi* BEHRENDSEN from Argentina are clearly indicative of the genus *Weyla.* However specimens in the GPIG, including what is apparently a type, clearly belong to the genus *Pseudopecten.* Notwithstanding this nomenclatural confusion it seems unwise at present to include the rather poorly preserved Göttingen specimens within *Ps. (Ps.) equivalvis* since they appear to differ from the latter by their greater convexity and smaller umbonal angle.

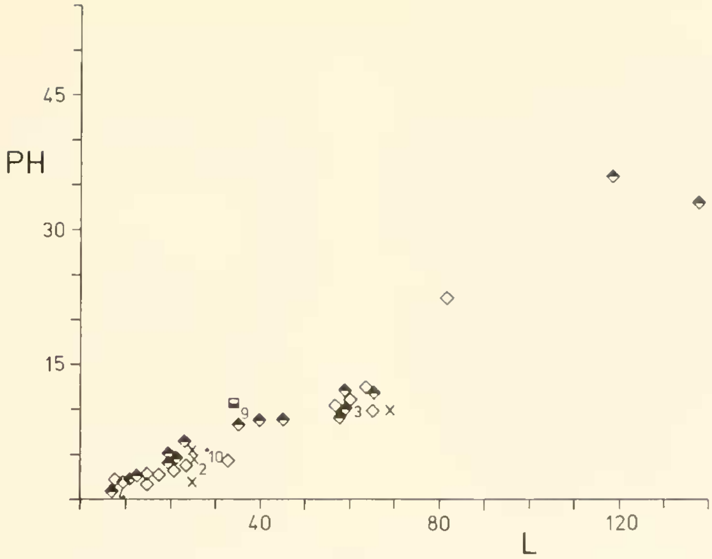


Text fig. 50: *Pseudopecten (Ps.) equivalvis* – anterior hinge length/length.

The figure of the left valve of *'P.' Johnstrupi* LUNDGREN closely resembles *Ps. (Ps.) equivalvis* in the number of plicae (20–25) and in H/UA, AH/L and PH/L (10). However, I_L/L and the umbonal angle of the right valve (70–80°) are low and may justify a separation, although the drawing could be inaccurate. The same may be true of *'P.' Zigoplocus* DI BLASI; FUCINI whose figure depicts a specimen with 22 plicae and H/UA (11) within the range of *Ps. (Ps.) equivalvis* but with an abnormally large I/L. DI BLASI's original description has proved impossible to trace.

'Aequipecten' bierringi from the L. Pliensbachian of Greenland was not figured or described by ROSENKRANTZ (1942). However it was said to closely resemble *'A.' aequivalvis* and it seems extremely likely that it is synonymous with J. SOWERBY's species.

'P.' acuticosta ROEMER is clearly a junior primary homonym of LAMARCK's species and as such should be rejected. The description leaves little doubt that ROEMER's hypodigm fell within the range of variation in *Ps. (Ps.) equivalvis.*



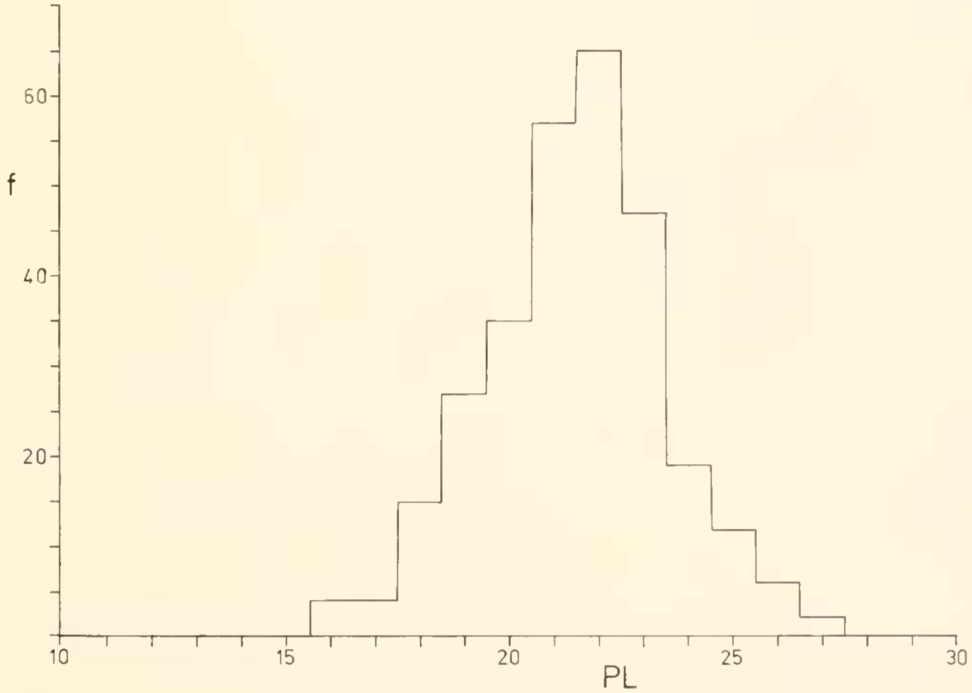
Text fig. 51: *Pseudopecten (Ps.) equivalvis* – posterior hinge length/length.

'*P.*' *priscus* Schlotheim; Dumortier has the down-sulcal tongueing of the growth lines typical of *Ps. (Ps.) dentatus* rather than *Ps. (Ps.) equivalvis*. '*P.*' *acutiradiatus* Münster; Dumortier is referable to the former species on the basis of the vertically striated disc flanks.

The great majority of authors have followed J. de C. Sowerby's alteration of the spelling of *equivalvis* to *aequivalvis* in vol. 6 of the 'Mineral Conchology' (1829). This is incorrect since J. Sowerby's original spelling in no way contravenes the ICZN rules and therefore must take historical precedence. However. *Ps. (Ps.) equivalvis* remains something of a misnomer because the shell is noticeably inequivalve.

5. STRATIGRAPHIC RANGE

Ps. (Ps.) equivalvis is first recorded in the Planorbis zone (Hettangian) of Lyme Regis (BM L62437), Dijon (DM 134), Lugano (Bistram, 1903) and Yorkshire (Tate and Blake, 1876). Subsequently it is recorded from the Angulata zone of E. France (Terquem and Piette, 1865) and the Bavarian Alps (Winkler, 1886) and the Bucklandi zone (L. Sinemurian) of Lyme Regis (BM L77272), the Rhone (Dumortier, 1867) and S. Bavaria (Schafhautl, 1851). *Ps. (Ps.) equivalvis* first occurs commonly in the middle Sinemurian Frodingham Ironstone (Semicostatum-Obtusum zones) and from then on it is widespread and often abundant until the U. Pliensbachian.



Text fig. 52: *Pseudopecten (Ps.) equivalvis* – frequency distribution for number of plicae.

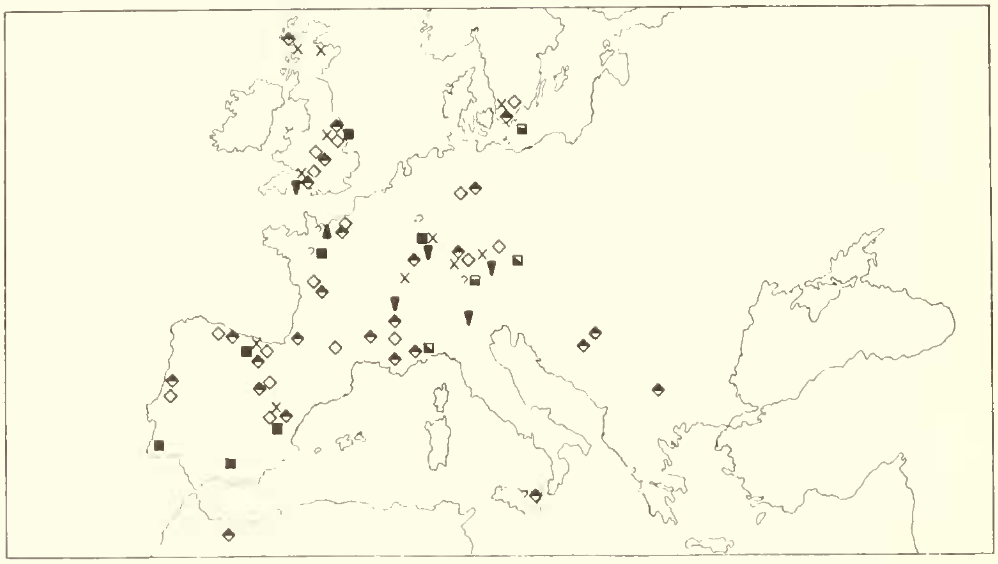
Extension of the range into the Tenuicostatum zone of the L. Toarcian is evidenced by material from the Cotswolds (OUM J33417-8) and Luxembourg (BSPHG). Most other Toarcian records (e. g. BM LL8142-3 from Lincolnshire, MNO 2073, 2073A-D; MNR B8689; MNP S00963 from N. France) are probably from this zone. However, HALLAM (1972) considered that the range extended into the middle Toarcian in Iberia and this horizon may be the source of some of the numerous Toarcian records from the area (e. g. BM LL30836; DAHM, 1965; DUBAR, 1925; VERNEUIL and COLLOMB, 1852). The species is recorded with *Hildoceras bifrons* in the W. Balkans (POMPECKJ, 1897) and YOUNG and BIRD (1828) report material from hard bands in the Alum Shale (Bifrons zone) of Yorkshire. In the latter area intensive field work by the author has failed to substantiate YOUNG and BIRD's claim. However, collecting from the Oolithe Ferrugineuse at Port-en-Bessin (Normandy) has brought to light a specimen (Pl. 2, Fig. 3) which may be a Bajocian representative of *Ps. (Ps.) equivalvis*. In the lack of further material and with the poor preservation of the available specimen the possibility still remains that it should more properly be referred to *Ctenostreon*.

Collecting at Snowshill Quarry, Gloucestershire has failed to substantiate AGER et al.'s (1973) record of *Pseudopecten* from the M. Bathonian of this locality. *Radulopecten vagans* and *Camptonectes (C.) laminatus* are the only pectinids present.

6. GEOGRAPHIC RANGE

Ps. (Ps.) equivalvis is found in all parts of Europe and there seem to be no obvious changes in distribution throughout its stratigraphic range (text fig. 53). There is thus no support for STAESCHE's (1926) view that small specimens (= '*Aequipecten*' *priscus*) originated in the Hettangian of the Rhone and subsequently spread to other parts of Europe in the Sinemurian.

Contrary to STAESCHE's opinion, *Ps. (Ps.) equivalvis* is not known throughout the world at any time. Records outside Europe are restricted to the Americas (text fig. 54) and the



Text fig. 53: *Pseudopecten (Ps.) equivalvis* – European distribution.

Text fig. 54: *Pseudopecten (Ps.) equivalvis* – World distribution (Pliensbachian reconstruction).

species is only known to be common in E. Greenland (Rosenkrantz, 1934, 1942). It is probably rare in S. America, Jaworski (1916) having recorded only two specimens and Steinmann (1881) a mere one, from Bolivia. It is by no means certain that the large number of fragments of *Ps. (Pseudopecten)* from S. America in the GPIG necessarily belong to *Ps. (Ps.) equivalvis* (see Section 4).

With regard to its range outside Europe, Hallam (1977) has suggested that the rarity of *Pseudopecten* at least in the W. Americas, may be due to competition with the ecologically similar aberrant pectinid *Weyla*. However, the absence of both *Weyla* and *Pseudopecten* from Asia, Australia and Antarctica remains to be explained.

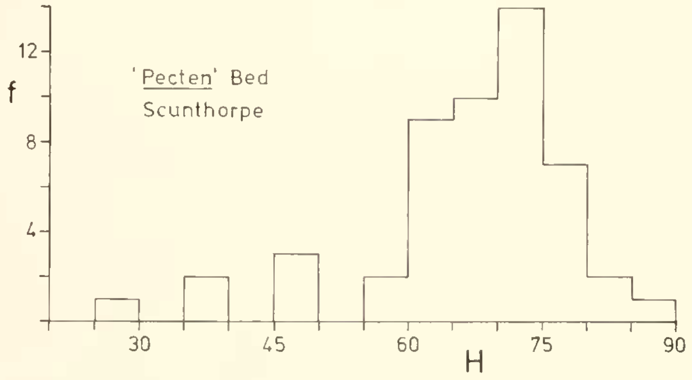
The observed distribution of *Ps. (Ps.) equivalvis* is most obviously explained by migration via the Canadian Arctic. However, there is now some evidence (see p. 25) to suggest that in the Pliensbachian a seaway existed between S. America, S. Africa and Antarctica (or perhaps between N. and S. America) and this could have afforded an alternative routeway.

7. DESCRIPTION OF ECOLOGY

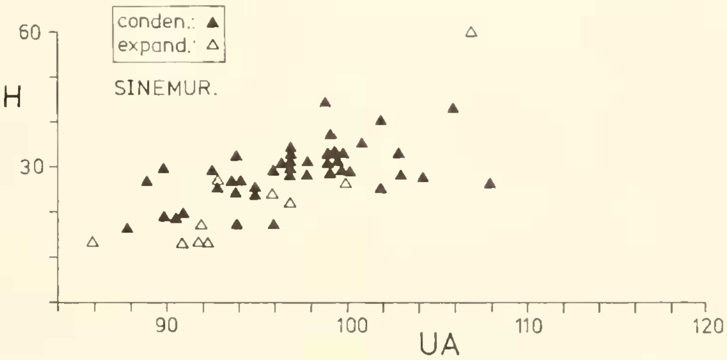
Ps. (Ps.) equivalvis first occurs commonly in the Frodingham Ironstone (Semicostatum-Obtusum zones), a stratigraphically condensed chamosite oolite in Lincolnshire. *Entolium (E.) lunare* is however a considerably more abundant element of the fauna, which also includes *Camptonectes (C.) subulatus, Chlamys (Ch.) textoria, 'Lima', Gryphaea, Astarte* and large *Cardinia* and ammonites. Most specimens of *Ps. (Ps.) equivalvis* are disarticulated and have, except in the umbonal region, rounded plicae (Pl. 2, Fig. 6). The maximum height attained is 45 mm (ScM). Contemporaneous specimens from more expanded, lower energy sequences such as the micritic limestones of S. Germany, reach only 25 mm in height while those from marls reach only 10 mm and are much less common (Staesche, 1926). All specimens from argillaceous facies have acute plicae and the limited available data suggests that they also have relatively large umbonal angles for their heights, compared to specimens from ironstones of the same age (text fig. 56). The associated fauna in the argillaceous facies is relatively deficient in *E. (E.) lunare* and large *Cardinia*.

L. Pliensbachian chamositic ironstone deposits such as the *'Pecten'* Bed (Ibex zone) of Lincolnshire, contain abundant *Ps. (Ps.) equivalvis* up to a maximum height of 90 mm (author's collection). All specimens are disarticulated and rest convex up, suggesting strong current activity. This is supported by the essentially unimodal size/frequency distribution obtained from a two sq. m. bedding-plane exposure (text fig. 55). Except in the region of the umbo, the plicae are rounded. Other faunal elements are less prominent than in the Frodingham Ironstone.

A high proportion of articulated specimens is indicative of lower energy conditions in the *'Pecten'* Bed (Ibex zone) of Blockley, Gloucestershire. The abundance of fish vertebrae and the siderite cement (Hewitt and Hurst, 1977) suggests a period of non-deposition. *Ps. (Ps.) equivalvis* attains a height (H: 78; OUM J17929) comparable to that in specimens de-



Text fig. 55: *Pseudopecten (Ps.) equivalvis* – frequency distribution for shell height in specimens collected from a 2 sq. m. bedding-plane exposure in the *'Pecten'* Bed (Ibex zone) of Lincolnshire.

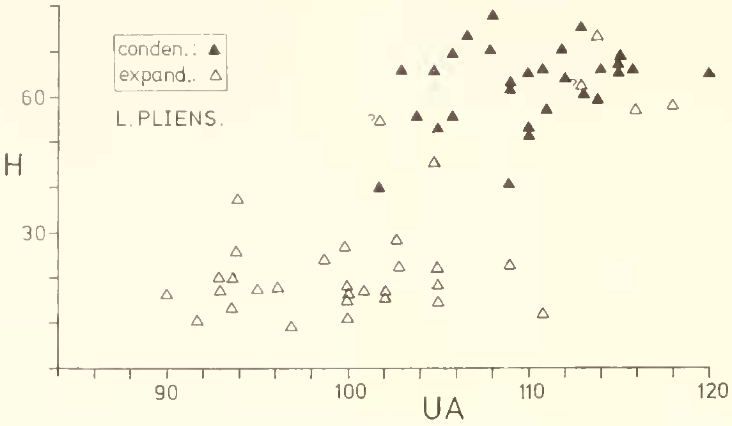


Text fig. 56: *Pseudopecten (Ps.) equivalvis* – height/umbonal angle for specimens from condensed and expanded sequences in the Sinemurian.

rived from contemporaneous high energy condensed deposits (see above) but the plicae remain, in contrast, angular at all ontogenetic stages (Pl. 2, Fig. 7). The associated fauna is deficient in *E. (E.) lunare* and is dominated by large specimens of *Astarte* and *Mactromya*. A variety of less common in- and epifaunal bivalves, gastropods and cephalopds attain a large size at this horizon (Hewitt and Hurst, 1977).

In contemporaneous low energy expanded sequences such as the Numismalis Mergel (Jamesoni/Ibex zones) of S. Germany, *Ps. (Ps.) equivalvis* is common but reaches a maximum height of only 37.5 mm (GPIT). In L. Pliensbachian clays in the English Midlands the maximum height is 27.5 mm (OUM J33290). All specimens have acute plicae. Larger specimens are occasionally recorded from predominantly clay sequences but these invariably turn out to be from storm lags at the top of small coarsening upward cycles (Sellwood, 1972). Thus specimens with rounded plicae reaching a maximum height of 60 mm (author's collection) occur in deposits of the Jamesoni zone at Robin Hood's Bay (Yorkshire) in association with *Camptonectes* (C.) *subulatus*, *Plicatula*, *Gryphaea*, *Gervillella* and exhumed *Pinna*.

In addition to their reduced maximum size, L. Pliensbachian specimens of *Ps. (Ps.) equivalvis* from uncondensed argillaceous facies also tend to have relatively large umbonal angles for their heights (text fig. 57). The few specimens that plot within the range of forms from condensed facies are almost certainly derived from thin, coarse grained horizons within predominantly clay sequences (see above).



Text fig. 57: *Pseudopecten (Ps.) equivalvis* – height/umbonal angle for specimens from condensed and expanded sequences in the L. Pliensbachian.

Ps. (Ps.) equivalvis is also common in the L. Pliensbachian of E. Greenland, where it occurs in coarse sands and limestones (Rosenkrantz, 1934, 1942), Raasay, where it is abundant in muddy sands (author's collection), and E. Spain, where it is found in bioclastic limestones (Behmel and Geyer, 1966). It is however conspicuous by its absence from the Jamesoni zone of the Pyrenees where condensed deposits contain common *Ps. (Ps.) dentatus* and the first European representatives of *Weyla* (Damborenea and Mancenido, 1979).

In the Sandy Series (Margaritatus zone) of the U. Pliensbachian in Yorkshire, *Ps. (Ps.) equivalvis* is common and reaches a maximum height of about 60 mm, while in the similarly expanded sequence of Raasay a maximum height of 70 mm is attained (author's collection). All specimens have rounded plicae. The associated fauna is dominated by *Oxytoma*, *Protocardia*, *Gryphaea* and the scaphopod *Dentalium*. *E. (E.) lunare* is rare but in a similar sedimentary and faunal association in the later parts of the Margaritatus zone in Dorset (Thorncombe Sands) it is common and *Ps. (Ps.) equivalvis* is rare. C. Palmer (1966b) remarked on the small size of specimens from a sandy limestone bed (Day's Shell Bed) at the top of the clay sequence (Eype Clay) representing the earlier parts of the Margaritatus zone in Dorset. They were said to reach only 25–30% of their 'normal' height. However, Palmer may have been drawing a comparison with specimens from Spinatum zone ironstones (see below) rather than with those from Margaritatus zone clays whose maximum height (30 mm; author's collection) is very probably *less* than that of Palmer's specimens. *Ps. (Ps.) equivalvis* is not known to be common in argillaceous facies anywhere in the U. Pliensbachian.

Ps. (Ps.) equivalvis is very common in the condensed, high energy, chamositic ironstones of the Spinatum zone in Lorraine, N. W. Germany and most parts of England. All specimens have rounded plicae (Pl. 2, Fig. 1) and the maximum height reached is 179 mm (BM 2662). The associated fauna is essentially the same as for the Margaritatus zone although in Northamptonshire, Oxfordshire and Somerset, where *Ps. (Ps.) equivalvis* is somewhat less common, *Ps. (Ps.) dentatus* and *Ps. (Ps.) veyrasensis* also occur. In S. Germany, the Spinatum zone is developed in a condensed but lower energy marlstone facies in which *Ps. (Ps.) equivalvis* usually exhibits acute plicae (Staesche, 1926) and attains a maximum height of 95 mm (GPIT). There are too few specimens available from uncondensed argillaceous facies to allow of any comparison in shape with forms from condensed or higher energy facies.

Ps. (Ps.) equivalvis is nowhere common after the U. Pliensbachian and over most of Europe its disappearance is correlated with the onset of bituminous shale deposition in the L. Toarcian. In parts of the W. Balkans and Iberian peninsula where the Toarcian is developed in high energy facies the species extends into the Bifrons zone (see Section 5). However, in similar facies in the Toarcian of E. Greenland (ROSENKRANTZ, 1934, 1942) and the Caucasus (POMPECKJ, 1897) the species seems to be absent. The largest Toarcian specimens are apparently to be found in the D'ORBIGNY Collection (H_{max}: 92; MNO 2073B). However, D'ORBIGNY's concept of the Toarcian may also have included parts of the U. Pliensbachian, so such records should be treated with caution.

Although quite widespread in the peri-Mediterranean region, *Ps. (Ps.) equivalvis* appears to reach large sizes only in high energy deposits such as the U. Pliensbachian calcarenites of the Iberian ranges (MENSINK, 1965), the sandy marls of the W. Balkans (POMPECKJ, 1897), the sandstones of Yugoslavia (UHLIG, 1884) and W. Bulgaria (TZANKOV and BONCEV, 1932) and the Toarcian marly oolites of the W. Balkans (POMPECKJ, 1897).

8. INTERPRETATION OF ECOLOGY

It is clear from Section 7 that *Ps. (Ps.) equivalvis* was a eurytopic species with respect to substrate, only clays formed under conditions of reduced oxygen tension constituting an unfavourable environment. It is also clear however, that there are correlations between the size and shape of *Ps. (Ps.) equivalvis* and the sediment grain size, rate of sedimentation and energy of the environment. Specimens from condensed deposits reach a large size, those from high energy environments having rounded plicae. Specimens from expanded high energy sandstone sequences reach a somewhat smaller maximum size and have rounded plicae. Specimens from expanded argillaceous sequences are much smaller, have acute plicae, and usually have a low H/UA ratio.

The correlation between high environmental energy and roundness of the plicae is most easily explained as the result of pre- and post-mortem abrasion of the originally angular plicae by wave and current-induced rolling of the shell.

The correlation between stratigraphic condensation and large size could be the consequence of one or more of the following factors:

a) High environmental energy. Most condensed sequences containing large *Ps. (Ps.) equivalvis* are developed as high energy chamosite oolites. In such environments the increased rate of supply of suspended food and dissolved oxygen might be expected to contribute to faster growth. However, the presence of comparably large specimens in a low energy horizon at Blockley seems to argue against this hypothesis.

b) Low turbidity condensed sequences are the result of decreased supply of sediment from suspension thus one can expect relatively clear water. This should lead to a reduction in the time required for cleaning the gills and defaecating and a consequent increase in the time spent feeding. Observations by the author on the extant species *Chlamys opercularis* reveal that high turbidity forces the animal to close the shell and abandon feeding, thus continuous high turbidity could be expected to markedly affect the growth rate. Slow sedimentation can also be expected to reduce turbidity (and thus enhance growth rate) by promoting the early diagenetic formation of a carbonate cement (HALLAM, 1972) which would inhibit resuspension of the sediment by lateral water movement. The fact that *Ps. (Ps.) equivalvis* attains a considerable size in expanded sandstone sequences does not however lend support to the view that the very large sizes attained in condensed sequences are simply the result of low turbidity. Neither can the latter easily explain the large sizes attained by presumably nektonic ammonites in condensed sequences.

c) Increased temperature. With the implicit assumption (given empirical support by the work of NICOL, 1967) that higher temperatures enable the development of large size, HEWITT and HURST (1977) have invoked climatic amelioration to account for the abnormally large sizes attained by molluscs at certain condensed horizons in the English Jurassic. In the case of *Ps. (Ps.) equivalvis* this fails to account for the small size of specimens in stratigraphically equivalent expanded sequences. However, HALLAM (1963) has suggested, on the basis of sedimentological evidence, that condensed ironstone formation may take place on shoals and that such environments may be warmer than surrounding deep water areas, characterised by clastic sedimentation. While such a model has the merit of explaining the large size of both benthos and nekton in condensed sequences, it suffers from a lack of actual evidence for increased temperature in the shoal environment. Until some independent evidence for the latter is obtained it seems advisable to adopt a composite theory (involving 2 and 3) to explain the correlation between condensed sequences and the development of large size in *Ps. (Ps.) equivalvis.* It has been assumed throughout that the latter is the consequence of relatively rapid growth. While this seems the most reasonable supposition and has a variety of plausible explanations (see above) the possibility cannot be entirely discounted that some undetected characteristic of the environment of condensed sequences (perhaps reduced predation) increased the length of life and thus allowed the development of larger sizes. An analysis of growth lines can be expected to provide a test for the assumption of faster growth.

The small size and low H/UA ratio of specimens from expanded argillaceous sequences is most easily interpreted as the result of relatively slow growth in conditions essentially opposite to those in the highly favourable condensed sequences. The local abundance of such 'stunted' specimens need not be viewed as evidence against this interpretation (see pp. 55, 124) and indeed 'stunting' may be an inappropriate term to use for the development of what are in fact adaptive shell features (see Section 9).

The lack of *Ps. (Ps.) equivalvis* in apparently highly suitable condensed facies containing *Weyla* in the Jamesoni zone of the Pyrenees is further evidence for HALLAM's contention (see p. 69) that *Pseudopecten* and *Weyla* were competitors. However, the occurrence of *Ps. (Ps.) dentatus* in the same deposits indicates that the competitive reaction did not extend to all *Pseudopecten* species. Indeed the inverse correlation in numbers or total mutual exclusion of *Ps. (Ps.) equivalvis* from *Ps. (Ps.) dentatus* in other areas (see p. 70) suggests that the absence of the former from deposits of the Jamesoni zone in the Pyrenees may be due more to competition with the latter species than with *Weyla*. *Ps. (Ps.) veyrasensis* has a similar distribution to *Ps. (Ps.) dentatus* and thus may also have had a competitive reaction with *Ps. (Ps.) equivalvis*. The frequent inverse correlation in numbers of *Ps. (Ps.) equivalvis* and *Entolium (E.) lunare* is strong evidence for competition. While in ironstones the dominant species appears to switch from the latter to the former after the Sinemurian there seems to be no secular change in sandstones, the dominant species at any one time or place being, therefore, presumably determined by priority.

9. FUNCTIONAL MORPHOLOGY

The strongly ornamented lower valve and quite thick shell of the large specimens of *Ps. (Ps.) equivalvis* common in high energy environments is paradigmatic for an adult reclining mode of life. The large byssal notch indicates that the juvenile obtained stability by means of byssal attachment. However, the allometric reduction in size of the notch indicates that byssal attachment was gradually abandoned during ontogeny. In the morphologically and ecologically similar extant species *Chlamys opercularis* byssal attachment effectively ceases at shell heights above 50 mm (SOEMODIHARDJO, 1974).

The relatively high convexity of the left valve is non-paradigmatic for reclining but is well suited to providing lift during swimming and combined with the ontogenetic increase in umbonal angle probably served to prolong this capacity until quite late stages in ontogeny.

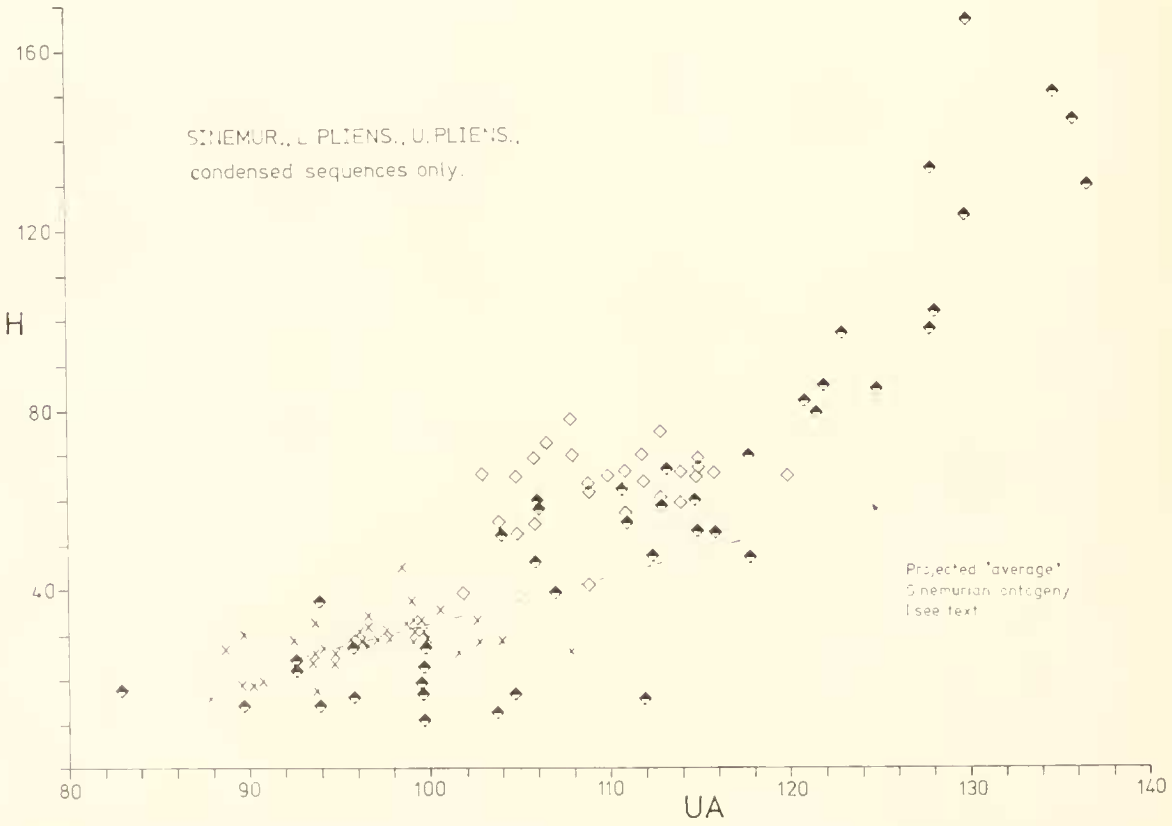
The small adult size and low H/UA ratio of specimens from expanded argillaceous sequences is adaptive for the environments represented by such sediments. Small size inhibits sinking into the soft substrate while both small size and a relatively large umbonal angle maximise the possibility of escape from sediment swamping by swimming, through maximising the trust/weight ratio of the shell.

Swimming ability in combination with a strongly plicate shell was also probably directed against attempted predation. The disadvantage of a plicate shell, in localising wear on the plical crests, was apparently offset by sub-plical shell thickening.

10. ORIGINS AND EVOLUTION

Undoubted specimens of *Ps. (Ps.) equivalvis* are known from the Planorbis zone so the origins of the species probably lie outside the Jurassic. However, no obvious ancestors present themselves.

Phyletic size increase is a very marked trend in *Ps. (Ps.) equivalvis*. However, the prevalence of ecophenotypic size variations (see Section 8) makes for great difficulty in the precise documentation of the trend. It is clear therefore that attention must be concentrated on the same environment at all stratigraphic levels. For this purpose the analysis is restricted to condensed sequences since these seem to represent the most clearly defined environment. Within the latter there is an increase in maximum height from 45 mm (Sinemurian) to 90 mm (L. Pliensbachian) to 179 mm (U. Pliensbachian). There may also be an associated acceleration in the development of H/UA since large L. and U. Pliensbachian specimens have H/UA values which plot above a projected 'average' Sinemurian ontogeny estimated from 'static' data (text fig. 58). However, the rather broad limits of the available data do not allow exclusion of the possibility that Sinemurian ontogenies in fact exhibit a much more rapid increase in H with



Text fig. 58: *Pseudopecten (Ps.) equivalvis* – height/umbonal angle for specimens from Sinemurian, and L. and U. Pliensbachian condensed sequences.

respect to UA thus the high H/UA values of at least large U. Pliensbachian specimens could represent no more than hypermorphic extension of Sinemurian allometry through the medium of phyletic size increase. Nevertheless, the H/UA values of moderate sized L. Pliensbachian specimens do seem to represent a genuine departure from Sinemurian ontogenies thus acceleration would appear to be evinced in at least the early stages of the phylogeny of *Ps. (Ps.) equivalvis*. If this is the case U. Pliensbachian H/UA values would seem to indicate subsequent *retardation* in the development of H/UA albeit only to the extent of returning ontogenies to a Sinemurian condition.

There is clearly a pressing need either for more 'static' data or for a 'dynamic' analysis of shape development using growth lines in order to facilitate a rigorous assessment of the role of heterochrony in the phylogeny of *Ps. (Ps.) equivalvis*.

Whether or not acceleration and subsequent retardation of shape development has occurred the fact remains that large U. Pliensbachian forms of *Ps. (Ps.) equivalvis* have relatively high H/UA ratios. As such they are mechanically inferior to earlier forms with respect to their design for swimming. This is difficult to interpret in conjunction with phyletic size increase. One might have expected evolution towards a more efficient, low H/UA, design in order to counteract the limitation on mobility and consequent susceptibility to predation imposed by increased size. (In living scallops a reduced ratio of muscle strength to body weight leads to the progressive loss of swimming ability as size increases during ontogeny [Gould, 1971; Soemodihardjo, 1974]; as a result escape from predators by flight eventually becomes impossible.) A resolution to this paradox may lie in the observation that some large sessile bivalves resist predation by the *absolute* strength of the adductor muscle. Thus Paine (1976) has observed that starfish are unable to prise apart the valves of *Mytilus* which are more than 8–10 cm in length. One may therefore perhaps infer that *Ps. (Ps.) equivalvis* gave up a fugitive policy towards the end of its stratigraphic range in favour of a policy of passive resistance. Such a strategy would only be worthwhile if large size could be achieved rapidly thus the hypothesis could be tested by an analysis of growth lines to see if faster growth was, in fact, characteristic of later populations. 'Static' data (see above) certainly allows that this may have been the case.

Phyletic increase in size, together with an apparent retardation in shape development and a reduction in tolerance of argillaceous substrates in the U. Pliensbachian (see Section 7) points to the prevalence of 'K' selection towards increased trophic efficiency. The high abundance of *Ps. (Ps.) equivalvis* in certain U. Pliensbachian chamosite oolites need not be viewed as evidence against this interpretation since it may well be the result of stratigraphic condensation.

The widespread development of unfavourable bituminous shale facies in the L. Toarcian undoubtedly caused a severe depletion of the numbers of *Ps. (Ps.) equivalvis*. The subsequent extinction of the species may have been the simple result of depletion to such an extent that re-establishment of self-supporting populations was impossible. However, it may also have been due to competition with one or more of the newly evolved, ecologically similar species, *Ps. (Echinopecten) barbatus*, *Propeamussium (P.) laeviradiatum* and *Entolium (E.) corneolum*.

Pseudopecten (Pseudopecten) dentatus
(J. de C. Sowerby 1827a)

Pl. 2, Figs. 11–14; text figs. 59–61, 62 (pars)

Synonymy

v* 1827a	*Pecten dentatus* sp. nov; J. de C. Sowerby, p. 143, pl. 574, fig. 1.
v 1833	*Pecten priscus* Schlotheim; Goldfuss, p. 43, pl. 89, fig. 5 (non Schlotheim sp.).
v 1833	*Pecten dentatus* J. de C. Sowerby; Goldfuss, p. 46, pl. 90, fig. 7.
1850	*Pecten dentatus* J. de C. Sowerby; d'Orbigny, v. 1, p. 285.
v non 1858	*Pecten dentatus* J. de C. Sowerby; Quenstedt, p. 753, pl. 92, fig. 3.
1860	*Pecten Thiollieri* sp. nov; Martin, p. 89, pl. 6, figs. 21–23.
1864	*Pecten Thiollieri* Martin; Dumortier, p. 62, pl. 10, figs. 4–7.
1864	*Pecten Euthymei* sp. nov; Dumortier, p. 64, pl. 10, figs. 8–10.
1867	*Pecten priscus* Schlotheim; Dumortier, p. 216, pl. 48, fig. 4 (non Schlotheim sp.).
1867	*Pecten dentatus* J. de C. Sowerby; Waagen p. 632.
1868	*Pecten Dieulafaiti* sp. nov; Jaubert, p. 234.
1869	*Pecten acutiradiatus* Münster; Dumortier, p. 135, pl. 21, fig. 8 (non Münster sp.).
? 1872	*Pecten Bersaskensis* sp. nov; Tietze, p. 106, pl. 6, fig. 3.
(?) 1876	*Pecten Thiollierei* Martin; Tate and Blake, p. 363.
(?) 1884	*Pecten Thiollieri* Martin; Simpson, p. 170.
? 1886	*Pecten Thiollieri* Martin; Winkler, p. 30.
? 1903	*Pecten (Chlamys) Thiollierei* Martin; Bistram, p. 33, pl. 2, figs. 13–15.
? 1904	*Chlamys aequiplicata* (Terquem); Cossmann, p. 503, pl. 16, fig. 15 (non Terquem sp.).
1909	*Pecten (Chlamys)* cf. *amphiarotus* Di Stefano; Trauth, p. 90, pl. 2, fig. 17.
? 1924	*Pecten dobbertinensis* sp. nov; Oertel, p. 564.
1925	*Pecten priscus* var. *Dieulafaiti* Jaubert; Dubar, p. 266, pl. 5, figs. 1–6.
(?) *1926*	*Chlamys Thiollieri* (Martin); Roman, p. 105.
1929	*Pecten (Pseudopecten) Dieulafaiti* Jaubert; Lanquine, p. 131, pl. 3, fig. 2.
1936	*Aequipecten thiollerei* (Martin); Dechaseaux, p. 40.
1936	*Aequipecten Euthymei* (Dumortier); Dechaseaux, p. 41.
1936	*Aequipecten priscus* var. *Dieulafaiti* (Jaubert); Dechaseaux, p. 42.
non 1948	*Pecten (Chlamys)* aff. *bersaskensis* Tietze; Dubar, p. 162, pl. 14, figs. 4a, 4b.
1948	*Pecten (Aequipecten) norigliensis* Tausch; Dubar, p. 163, pl. 13, fig. 12 (non Tausch sp.).
1948	*Pecten (Aequipecten) semiarticulatus* G. Meneghini; Dubar, p. 216, pl. 28, figs. 22–25, text fig. 53 (non G. Meneghini sp.).
(?) *1950*	*Chlamys Thiollerei* (Martin); Roman, p. 25.
1966	*Aequipecten dieulafaiti* (Jaubert); Behmel and Geyer, p. 28.
1973	*Chlamys (Aequipecten) Thiollerei* (Martin); Lentini, p. 28, pl. 15, fig. 6.

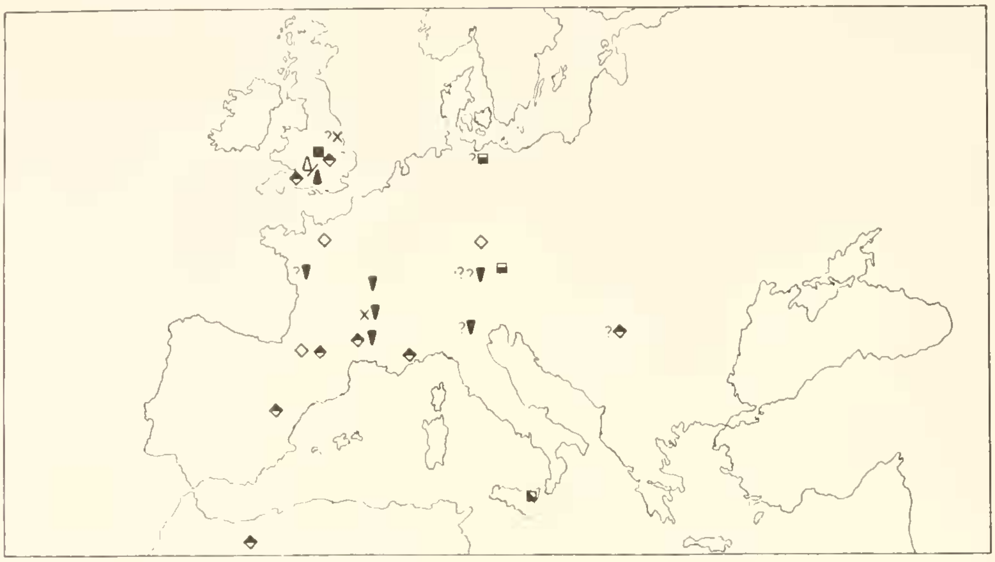
Lectotype of *Pecten dentatus* J. de C. Sowerby 1827a, p. 143, pl. 574, fig. 1 designated herein; BM 20719; Pl. 2, Figs. 11, 12 herein; H: 55, L: 58, UA: 109, PL: 20; gravels derived from M. Lias (U. Pliensbachian), Bugbrook, Northamptonshire.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

'Nearly orbicular, convex, minutely striated concentrically, ribbed; ribs about twenty close, large, angular, obtuse; ears defined, small; margin deeply toothed; valves similar.

The peculiar characters of this *Pecten* are the sharp projection of the edge between each rib and the flat inclined sides of each rib.

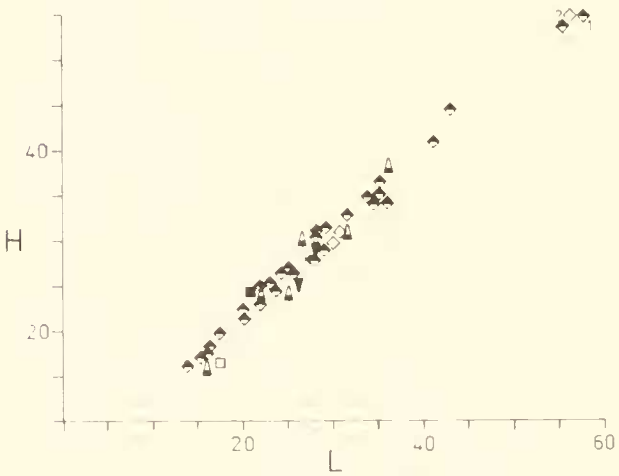
Several specimens of this fossil are in the collection of Miss Baker, who found them in transported fragments of limestone, in what are there called gravel pits, at Bugbrook and Staverton, in Northamptonshire. It also occurs in the valley of Catmus in Rutlandshire. The figure is taken from a specimen which has both valves, but wants the ears; they are supplied from another, in other respects inferior, individual.'



Text fig. 59: *Pseudopecten (Ps.) dentatus* – European distribution.

2. AMENDED DIAGNOSIS

Distinguished from *Ps. (Ps.) equivalvis* by the higher, vertically striated, disc flanks (Pl. 2, Fig. 13) and down-sulcal tongueing of the comarginal striae (Pl. 2, Figs. 11, 12). Distinguished from *Ps. (Ps.) veyrasensis* by the larger modal number of plicae (17/18 cf. 14).

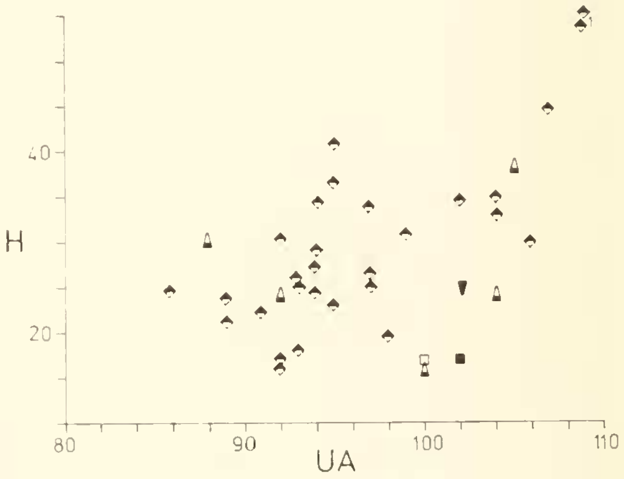


Text fig. 60: *Pseudopecten (Ps.) dentatus* – height/length.

3. AMENDED DESCRIPTION

Essentially similar to *Ps. (Ps.) equivalvis* apart from the diagnostic features (see Section 3), smaller maximum height 70 mm; Dubar, 1925), greater convexity, acute angle between the anterior auricles and the hinge line, obtuse angle between the posterior auricles and the hinge line, and the ornament. Both valves ornamented with between 16 and 20 (most commonly 17 or 18) radial plicae (text fig. 62), rounded on the right valve, angular on the left. Usually one more plica on left valve than right; plicae occasionally bearing lamellae near the anterior and posterior margins.

Metric proportions are plotted in text figs. 60, 61.

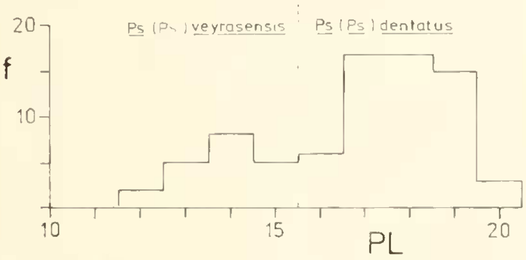


Text fig. 61: *Pseudopecten (Ps.) dentatus* – height/umbonal angle.

4. DISCUSSION

The lectotype (herein designated) of *'Pecten' dentatus* J. de C. Sowerby (BM 20719; Pl. 2, Figs. 11, 12; 1) is a large, somewhat atypical, form with 20 plicae. It has moreover suffered post-mortem compression such that the characteristic features of high disc flanks and convexity are not apparent. However, the diagnostic ventral tongueing of the sulcal growth lines is visible and leaves no doubt that the specimen should be the name bearer for the species described in Section 3. *'P.' priscus* Schlotheim; Goldfuss (non Schlotheim) also exhibits this feature while *'P.' acutiradiatus* Münster; Dumortier (non Münster) has the vertically striated disc flanks diagnostic of *Ps. (Ps.) dentatus*.

'P.' Thiollieri Martin was said to have 20 plicae but the figures show only 17 or 18 as is typical of *Ps. (Ps.) dentatus*. Moreover, the characteristic convexity and disc flank ornament of the latter species is well displayed. Similarly, *'P.' Thiollieri* Martin; Winkler was also said to have 20 plicae but a specimen (BSPHG) collected from the same horizon and locality as Winkler's, exhibits only 16 plicae. Records of Martin's species in Dechaseaux (1936) and Lentini (1973) refer to specimens with, respectively, vertically striated disc flanks and ventrally tongueing sulcal growth lines, as in *Ps. (Ps.) dentatus*. However, specimens referred to Martin's species by Bistram (1903) appear to have curvilinear growth lines and 21 plicae, as in *Ps. (Ps.) equivalvis*. In view of the evident possibility of confusion with the latter species, inadequately described and unillustrated records of Martin's species in Tate and Blake (1876), Simpson (1884) and Roman (1926, 1950) can only be tentatively synonymised with *Ps. (Ps.) dentatus*. However, examples of Martin's species with 20 plicae and the disc flank ornament and convexity characteristic of *Ps. (Ps.) dentatus* are clearly figured and reported to be common by Dumortier (1864). It may therefore be that the mean (and perhaps range) in the number of plicae was higher early in the stratigraphic range of the species.



Text fig. 62: *Pseudopecten (Ps.) veyrasensis/dentatus* – frequency distribution for number of plicae.

'P.' Euthymei Dumortier has the characteristic disc flank and sulcal ornament of *Ps. (Ps.) dentatus* and the number of plicae (16) is within the range of variation in the latter species.

'P.' Dieulafaiti Jaubert was erected for a specimen originally referred to *'P.' priscus* Schlotheim by Dumortier (1867). The number of plicae (17) and the down sulcal tongueing of the growth lines indicate its identity with *Ps. (Ps.) dentatus*. Subsequent varietal use of the name does not depart from Jaubert's hypodigm.

'P.' Bersaskensis Tietze was erected for a single specimen which was said to have 16 plicae, thus suggesting that it may be conspecific with *Ps. (Ps.) dentatus*. However, the width of the sulci and shallowness of the byssal notch may justify a specific separation. Indeed, only 15 plicae are depicted in the figure and this together with the fact that Dubar (1948) has applied Tietze's specific name to forms with 14 plicae, suggests that *'P.' Bersaskensis* may be a synonym of *Ps. (Ps.) veyrasensis*.

'Chlamys' cf. *aequiplicata* (Terquem); Cossmann (non Terquem) has 16 plicae but the small size of the figured specimen does not allow an unequivocal specific determination.

'P.' ('Ch.') cf. *amphiarotus* Di Stefano; Trauth (non Di Stefano) was applied to 8 specimens possessing between 17 and 19 plicae, moderate convexity and ventrally tongueing sulcal growth lines as in *Ps. (Ps.) dentatus*.

'P.' dobbertinensis Oertel was separated from *'P.' aequivalvis* J. Sowerby by the reduced number of plicae (17) and greater convexity. Although a figure was not provided this is strongly suggestive of equivalence with *Ps. (Ps.) dentatus*.

The names *'P.' ('Aequipecten') noriglicnsis* Tausch (non Tausch) and *'P.' ('Ae.') semiarticulatus* G. Meneghini (non G. Meneghini) were applied by Dubar (1948) to specimens with, respectively, 16 and 17 plicae. In both cases the down-sulcal tongueing of the comarginal ornament indicates that they should be included within *Ps. (Ps.) dentatus*.

Quenstedt's (1858) use of J. de C. Sowerby's specific name is for a specimen (GPIT 2-92-3; Pl. 6, Fig. 12) which is clearly a representative of the 'coarse' phenotype of *Chlamys (Ch.) textoria*.

5. STRATIGRAPHIC RANGE

Ps. (Ps.) dentatus first occurs in the Planorbis zone (Hettangian) when it is locally common. In like manner it is found in all stages until the U. Pliensbachian. Toarcian records are limited to two specimens from Adderbury, Oxon (BM L30490) which are almost certainly from the lower part of the stage. However, *Ps. (Ps.) dentatus* returns in moderate numbers in the Aalenian/Bajocian. A single specimen from the Parkinsoni zone (BM L77551) is the last known representative of the species.

6. GEOGRAPHIC RANGE

Ps. (Ps.) dentatus occurs sporadically over the whole of the European region (text fig. 59) but is unknown from the rest of the world. Within Europe the patchy distribution of the species is probably at least in part due to the localised development of the favoured condensed sedimentary facies (see Section 8). However, gradual migration from an initial Hettangian base in S. Europe may also have controlled distribution. In the Sinemurian the species is only common in the Rhone (Dumortier, 1867) yet apparently suitable condensed facies are well developed in, for instance, the Frodingham Ironstone of Lincolnshire. The only records from N. Europe during the Sinemurian are from clays of the Bucklandi zone in Yorkshire (Tate and Blake, 1876; Simpson, 1884). L. Pliensbachian records are more widespread in continental Europe yet *Ps. (Ps.) dentatus* is again conspicuous by its absence from condensed deposits in England (e. g. the *'Pecten'* Beds of Blockley, Glos., and Scunthorpe, Lincs.). With reference to a hypothetical migration it should however be noted that the foregoing examples are of horizones in which *Ps. (Ps.) equivalvis*, a possible competitor (see Section 8), is abundant.

In the U. Pliensbachian the range of *Ps. (Ps.) dentatus* extended north to include England and also spread south to Morocco (DUBAR, 1948). However, in the M. Jurassic the species was restricted to England despite the development of apparently suitable condensed facies, lacking in *Ps. (Ps.) equivalvis*, in other areas (e. g. S. Germany and France).

7. DESCRIPTION OF ECOLOGY

Ps. (Ps.) dentatus is quite common in the Planorbis zone (Hettangian) of the Rhone basin where it reaches a maximum height of 35 mm (DUMORTIER, 1864). A general impression gained from the literature is that forms with plical counts in the upper part of the range of variation may be more common than at later horizons in the stratigraphic range (see Section 4). The associated sediments are ferruginous limestones with a diverse fauna of ammonites, crinoids and corals together with the bivalves *Chlamys (Ch.) valoniensis*, *Ch. (Ch.) pollux*, *Plagiostoma*, *Plicatula* and *Cardinia*. In the same region *Ps. (Ps.) dentatus* becomes very common in the Oxynotum zone (Sinemurian) which is represented by a maximum of 8 m of limestone. Large, well preserved specimens occur with abundant '*Terebratula*', ammonites and the bivalves *Cardinia* and *Gryphaea* (DUMORTIER, 1867).

In the Jamesoni zone (L. Pliensbachian) of the Pyrenees, *Ps. (Ps.) dentatus* is locally common enough to form lumachelles containing specimens up to a maximum height of 70 mm (DUBAR, 1925). In this region the whole substage is condensed into a 2–3 m succession containing abundant ammonites and the pectinids *Ch. (Ch.) textoria*, *Entolium (E.) lunare and Weyla*. *Ps. (Ps.) equivalvis* is notable by its absence.

Ps. (Ps.) dentatus occurs abundantly in reefal deposits in the U. Pliensbachian of Morocco where it is associated with corals, algae, brachiopods and large bivalves of the genera *Lithiotis*, *Opisoma* and *Pachyrisma* (DUBAR, 1948). *Ps. (Ps.) veyrasensis* also occurs but *Ps. (Ps.) equivalvis* is absent. *Ps. (Ps.) dentatus* is found, albeit rather less commonly, in nonreefal micritic limestones in N. Africa and Provence where it is often associated with accumulations of rhynchonellid and terebratulid brachiopods (LANQUINE, 1929). In the U. Pliensbachian of England, *Ps. (Ps.) dentatus* only occurs in any numbers in deposits of the Spinatum zone in Oxfordshire, Northamptonshire and Somerset, where it reaches a maximum height of 55 mm (BM 20719). The sediments are chamositic oolites, locally sandy, containing a fauna dominated by the brachiopods *Tetrarhynchia tetrahedra* and *Lobothyris punctata*. *E. (E.) lunare*, *Ps. (Ps.) veyrasensis* and *Ps. (Ps.) equivalvis* also occur but the last is much less common than in contemporaneous deposits further north (e. g. Cleveland Ironstone) where *Ps. (Ps.) dentatus* is absent.

In the M. Jurassic *Ps. (Ps.) dentatus* is only known to occur in any numbers in the condensed ironshot limestones of the Aalenian/Bajocian in Somerset and Dorset where it attains a maximum height of 38 mm (BM 52121). The associated fauna is dominated by terebratulid and rhynchonellid brachiopods and the bivalves *Astarte*, *Pholadomya* and *Trigonia*.

Apart from the occurrences discussed above *Ps. (Ps.) dentatus* is a rare species. When it is found over a broad palaeolatitudinal range, as in the U. Pliensbachian, the species seems to be more common towards the south.

8. INTERPRETATION OF ECOLOGY

It is apparent from Section 7 that environments of relatively high temperature and low turbidity were favourable to *Ps. (Ps.) dentatus*. The former view is evidenced by the relative abundance of the species in low palaeolatitudes while the latter view is evidenced by the large size and frequent abundance in condensed sequences where a combination of slow sedimentation and early diagenetic cement formation probably reduced turbidity (see p. 71). The association with hermatypic corals, which are unable to tolerate high turbidity, can presumably be explained on the same basis, while the extreme rarity of the species in the Toarcian can be seen to be the consequence of the widespread development of expanded clay facies, producing turbid waters and possibly soupy substrates.

Reef deposits and some of the condensed sequences (e. g. M. Lias chamosite oolites and the Aalenian/Bajocian ironshot limestones of England) were probably characterised by high environmental energy as well as low turbidity. However, others (e. g. those in the L. Lias of S. France) were probably formed under more tranquil conditions, indicating that rapid water movement was not a prerequisite for *Ps. (Ps.) dentatus*. Indeed the absence of the species from a number of apparently suitable condensed sequences (see Section 6) coupled with its occasional presence, in moderate numbers, in expanded limestone sequences suggests that low turbidity may not have been the sole or even most important factor controlling distribution. The association with numerous brachiopods in both high and low energy environments is unusual for a Jurassic pectinid and some reliance on the presence of the latter group, perhaps for provision of firm substrates for the byssal attachment of the juvenile (see Section 9), may thus explain the localised occurrence of *Ps. (Ps.) dentatus*. Another explanation may be provided by competition with the eurytopic species *Ps. (Ps.) equivalvis* whose numbers are inversely correlated with those of *Ps. (Ps.) dentatus* in sediments whose physical environment of deposition would appear to have been suitable for both species. Competition with *Ps. (Ps.) equivalvis* in such environments could account for the rarity of *Ps. (Ps.) dentatus* in the L. Lias of N. Europe and thus obviate the need to invoke a migration from a more southerly source (see Section 6). There is no evidence for competition with *Ps. (Ps.) veyrasensis*, *Entolium (E.) lunare*, *Chlamys* or *Weyla* (see p. 71).

It must be admitted that a unified explanation for the patchy distribution of *Ps. (Ps.) dentatus* is still wanting and a more detailed study of its palaeoecology might be expected to reveal some critical aspect of stenotopy which has hitherto gone undetected.

9. FUNCTIONAL MORPHOLOGY

In *Ps. (Ps.) dentatus* moderate adult size and shell thickness appear to represent a compromise between the opposing paradigms for reclining in both high and low energy environments. The firm substrates usually occupied under such conditions (see Section 8) perhaps also allowed the development of a relatively convex shell with its attendant strengthening and stiffening attributes by reducing the danger, to which such a shape is susceptible, of sinking into the substrate. The increased mechanical efficiency thus acquired could account for the smaller number of plicae relative to the less convex species *Ps. (Ps.) equivalvis*. The occasional presence of *Ps. (Ps.) dentatus* in expanded micrite sequences does not however support the foregoing interpretation of morphology as an adaptation to a reclining mode of life. The moderate shell size and convexity would have been poorly suited to reclining on the relatively soft substrates afforded by such sediments. Moreover, the large juvenile byssal notch indicates that *Ps. (Ps.) dentatus* was byssate for at least the early part of its ontogeny. The subsequent relative reduction in the size of the notch indicates that this ability was gradually lost but in the morphologically similar Recent species *Argopecten gibbus (= Aequipecten gibbus nucleus)* byssal attachment continues to shell heights of 35 mm (Stanley, 1970). It may therefore be that at least early representatives of *Ps. (Ps.) dentatus* (see Section 7) were byssate throughout life.

10. ORIGINS AND EVOLUTION

Since *Ps. (Ps.) dentatus* is recorded in the Planorbis zone its origins must be sought before the Jurassic. '*Pecten*' *coronatiformis* Krumbeck (1924) a species described from the U. Trias of Timor with vertically striated disc flanks and ventrally tongueing growth lines in the sulci, seems the most likely ancestor. Krumbeck's species differs from *Ps. (Ps.) dentatus* only in the possession of angular plicae on the right valve and rounded plicae on the left valve.

Within *Ps. (Ps.) dentatus* maximum height shows no significant overall phyletic change in the passage from the Hettangian (30 mm) to the L. Pliensbachian (70 mm) to the U. Pliensbachian (55 mm) to the Aalenian/Bajocian (38 mm). There is, however, limited evidence (see Section 4) for phyletic change in the pattern of plical variability, Hettangian populations seeming to have a higher mean number of plicae. Later populations may have been subject to character displacement consequent upon competition with *Ps. (Ps.) equivalvis* (see Section 8), a species having a higher modal number of plicae (22 cf. 17/18) which only became abundant in the Sinemurian. Much more detailed analysis of Hettangian populations is needed to establish the reality of the phyletic change and a test of the character displacement hypothesis through an analysis of Aalenian/Bajocian populations (which, if character displacement has been operative, should show an increased mean number of plicae due to the decline of *Ps. (Ps.) equivalvis)* is also required. The lack of an obvious functional basis for character displacement in this example need not be viewed as evidence against its action. Most reported cases (e. g. Russell, 1972; Schindel and Gould, 1977) can only be explained by invoking selection of a pleiotropic gene which also codes for a significant but undetected physiological difference.

It is by no means clear how an apparently stenotopic and geographically restricted species such as *Ps. (Ps.) dentatus* managed to re-establish itself after a drastic reduction in numbers through the widespread development of unfavourable facies in the Toarcian, when the relatively eurytopic and cosmopolitan *Ps. (Ps.) equivalvis* suffered a similar decline which apparently led to its extinction (see p. 73). Neither is a convincing deterministic explanation available to account for the Bajocian extinction of *Ps. (Ps.) dentatus* although it could relate to the extinction of some commensal species (see Section 8).

Pseudopecten (Pseudopecten) veyrasensis (Dumortier 1864)

Pl. 2, Figs. 19–21; text figs. 62 (pars), 63

Synonymy

? 1855	*Pecten aequiplicatus* sp. nov; Terquem, p. 323, pl. 23, fig. 5.
1864	*Pecten veyrasensis* sp. nov; Dumortier, p. 163, pl. 24, fig. 15.
1869	*Pecten Julianus* sp. nov; Dumortier, p. 307, pl. 40, fig. 1.
1869	*Pecten Humberti* sp. nov; Dumortier, p. 308, pl. 40. fig. 2.
? 1872	*Pecten Bersaskensis* sp. nov; Tietze, p. 106, pl. 6, fig. 3.
1878	*Pecten heterotus* sp. nov; Gemmellaro and Di Blasi in Gemmellaro, p. 391, pl. 30, figs. 3–5.
1878	*Pecten isoplocus* sp. nov; Gemmellaro and Di Blasi in Gemmellaro, p. 392, pl. 30, figs. 6, 7.
1886	*Pecten Seguenzae* sp. nov; Di Stefano, p. 135, pl. 4, figs. 31–33.
1892	*Pecten convexus* Parona; Parona, p. 16, pl. 1, fig. 4.
non 1904	*Chlamys aequiplicata* (Terquem); Cossmann, p. 503, pl. 16, fig. 15.
1926	*Chlamys Humberti* (Dumortier); Roman, p. 113.
1929	*Pecten (Pseudopecten) julianus* Dumortier; Lanquine, p. 131.
1932	*Pecten* cf. *Julianus* Dumortier; Tzankov and Boncev, p. 231, pl. 1, fig. 10.
non 1936	*Aequipecten aequiplicatus* (Terquem); Dechaseaux, p. 41.
1948	*Pecten (Chlamys)* aff. *bersaskensis* Tietze; Dubar, p. 162, pl. 14, figs. 4a, 4b.
1948	*Pecten (Aequipecten) Julianus* Dumortier; Dubar, p. 163, pl. 13, figs. 13a, 13b.
non 1973	*Chlamys (Aequipecten) aequiplicata* (Terquem); Lentini, p. 27, pl. 15, fig. 3.

The type material of *Pecten Veyrasensis* Dumortier 1864, p. 163, pl. 24, fig. 15 may be in MHNL. Dumortier cites the following dimensions: H: 20, L: 20, C/2: 5, UA: 93. The material was derived from the M. Lias (U. Pliensbachian) of Ardèche.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

'Testa orbiculari, compressa, costata, costis circa 13 angulatis latis, rugis transversis impressis, quae in medio costarum angulosae sursum ascendunt, intervallis profunde impressis, foraminatis.

Dimensions: longeur 20 millim., largeur 20 millim., épaisseur 5 millim. $^1/_2$, ouverture de l'angle apical 93°.

Coquille arrondie, épaisse, portant environs 13 côtes, grosses, carenées, ornées de rides saillantes, en chevrons, dont le sommet est dirigé en haut. Les sillons qui séparent les Côtes sont étroits et profonds, et comme les chevrons qui ornent les côtes viennent s'y rencontrer, il en resulte que ces sillons ne sont qu'une serie de petites cavités resserrées entre les extremités de ces chevrons. Entre la dernière côte et la bord de la coquille il existe une petite aréa, ornée de striés transverses.

Le bord cardinal est droit – L'oreille anterieure grande, ornée de striés verticales sinueuses et fortement enchancrée pour le passage du byssus: oreille posterieure... La coquille est fortement sinueuse dans la région palleale. Ce *Pecten* est précieux, parce que grace sa livrée riche et compliquée, il est toujours reconnaissable, même dans ces fragments. Il paraît spécial aux dépôts de l'Ardèche: je l'ai recueilli a Veyras, dans les couches remplies de tiges du *Neuropora socialis*, si remarquable de cette localité.

Localité: Veyras. r. Explication de la figure: Pl. XXIV, fig. 15, *Pecten Veyrasensis* de Veyras, grossi deux fois. De ma collection.'

2. AMENDED DIAGNOSIS

Distinguished from *Ps. (Ps.) dentatus* and *Ps. (Ps.) equivalvis* by the lower modal number of plicae (14 cf. 17/18 and 22 respectively) and from the latter also by the vertically striated disc flanks and down-sulcal tongueing of the comarginal striae.

3. AMENDED DESCRIPTION

Essentially similar to *Ps. (Ps.) dentatus*, differing only by the diagnostic feature (see Section 2), the range of plical variation (12–15, text fig. 62) and by the tendency to develop a rectilinear plical form on the shell interior (Pl. 2, Fig. 21). The maximum height is 74.5 mm (GPIG).

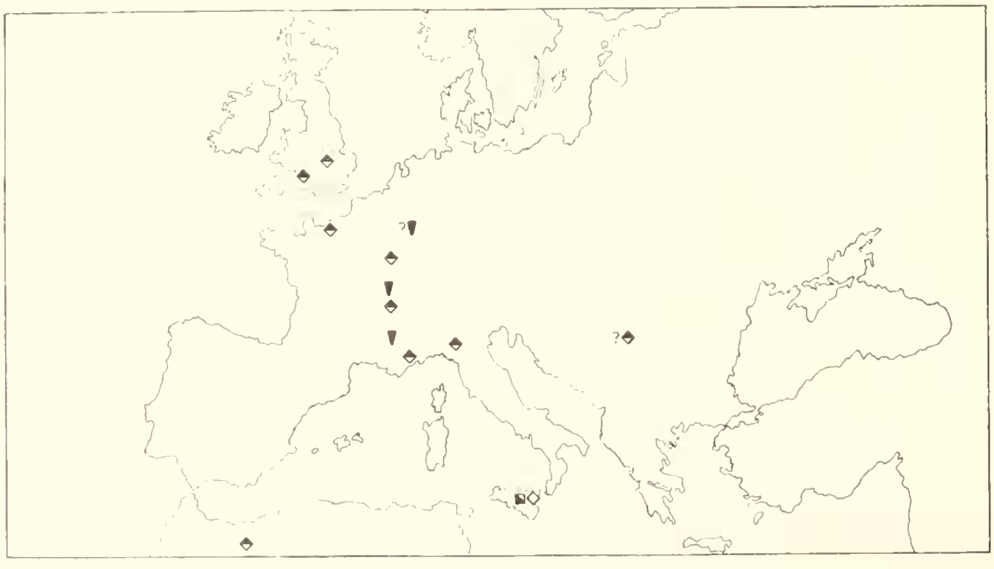
4. DISCUSSION

The specific name applicable to the range of forms making up the left-hand peak of text fig. 62 is a matter of some uncertainty. Apparently, the earliest description of a species within the 12–15 plicae range is '*Pecten*' *aequiplicatus* Terquem. Although the text specifies the relatively uncommon number of 12 plicae the figure illustrates a more typical specimen with 15 plicae. However, Terquem also referred to small spines on the left valve and subsequent applications of the name, by authors who may have had access to the type material, have been to forms with 12 plicae and spines (Dechaseaux, 1936) or 10 plicae (Lentini, 1973) which suggest that '*P.*' *aequiplicatus* is a poorly figured junior synonym of *Spondylopecten (Plesiopecten) subspinosus*. In contrast, Cossmann (1904) has figured a specimen with 16 plicae under Terquem's species which suggests that '*P.*' *aequiplicatus* is an extreme variant of *Ps. (Ps.) dentatus*. In view of this ambiguous usage and in the lack of knowledge concerning the whereabouts of the type material, it seems best to rule out Terquem's species as a candidate for the name of the species described in Section 3. The next available name is '*P.*' *Veyrasensis* Dumortier. The original description (see Section 1) specifies 13 plicae although the figure shows a more typical number of 14. Dumortier's species '*P.*' *Julianus* and '*P.*' *Humberti*, with 12 and 14 plicae respectively, fall within the range of variation and exhibit no other distinguishing features.

The original description of '*P.*' *Bersaskensis* Tietze specifies 16 plicae (outside the range of *Ps. (Ps.) veyrasensis)* but since the figure depicts only 15 plicae and specimens with 14 plicae are referred to Tietze's species by Dubar (1948), it is possible that '*P.*' *Bersaskensis* is a synonym of *Ps. (Ps.) veyrasensis*. However, the width of the sulci and shallowness of the byssal notch may justify a distinction, although this appearance could be due to reversed printing of a copper engraving (see p. 17).

'*P. heterotus* and '*P.*' *isoplocus* Gemmellaro and Di Blasi exhibit 13–14 and 14 plicae respectively, and both have the moderately high disc flanks, rounded right valve plicae and angular left valve plicae characteristic of *Ps. (Ps.) veyrasensis*. '*P.*' *Seguenzae* Di Stefano with 14–15 plicae is similarly inseparable.

The original description of '*P.*' *convexus* Parona has proved impossible to trace but Parona's (1892) subsequent use of the name is for a specimen whose figure is indistinguishable from *Ps. (Ps.) veyrasensis*.



Text fig. 63: *Pseudopecten (Ps.) veyrasensis* – European distribution.

5. STRATIGRAPHIC RANGE

Ps. (Ps.) veyrasensis apparently first occurs in the Angulata zone (Hettangian) of the Rhone, where it is fairly common (Dumortier, 1864). There are no unequivocal Sinemurian records although numerous specimens are recorded from an unspecified horizon in the Hettangian/Sinemurian sequence of Sicily (Gemmellaro, 1878). L. Pliensbachian records are restricted to 6 specimens (BM L92958-63) from the Jamesoni zone of the latter area but the species becomes locally quite common again in the U. Pliensbachian. There are no records after the Spinatum zone.

6. GEOGRAPHIC RANGE

Ps. (Ps.) veyrasensis is unknown outside the European region. Within Europe (text fig. 63) the limited available data (with unequivocal Hettangian records being restricted to the Rhone and U. Pliensbachian records extending from Morocco to England) suggests a distribution pattern mirroring that of *Ps. (Ps.) dentatus*, thus a northward migration may have occurred (however see p. 76).

7. DESCRIPTION OF ECOLOGY

Ps. (Ps.) veyrasensis is quite common in the condensed ironshot lumachelle (Angulata zone) of the northern Rhone basin where it attains a maximum height of 27 mm (DM). The diverse associated fauna includes *Entolium (E.) lunare*, *Pinna*, *Plicatula* and *Cardinia*. In the Hettangian/Sinemurian of Sicily, Gemmellaro (1878) records 23 specimens of *Ps. (Ps.) veyrasensis* (H_{max}: 20) from limestones with a diverse neritic fauna dominated by gastropods, the bivalve '*Modiola*', and the brachiopods *Spiriferina* and *Rhynchonella*. From the same area Di Stefano (1886) records *Ps. (Ps.) veyrasensis* from an unspecified horizon in the Trias/L. Lias. 6 specimens (BM L92958-63) labelled 'Jamesoni zone, Sicily' may have been the basis for Di Stefano's record and allow a more accurate stratigraphic positioning since they are named '*P.' Seguenzae*, his synonym for *Ps. (Ps.) veyrasensis* (see Section 4). Di Stefano describes an associated fauna consisting mainly of ammonites, spiriferid, terebratulid and rhynchonellid brachiopods and the bivalves *Entolium (E.) lunare*, *Oxytoma*, *Pinna*, *Plicatula*, *Modiolus* and *Pholadomya*.

In the U. Pliensbachian of Morocco *Ps. (Ps.) veyrasensis* occurs in reefal deposits (fauna p. 76) where it reaches a height of ca. 30 mm (Dubar, 1948). *Ps. (Ps.) dentatus* is a notable associate, as it is in non-reefal micrites in N. Africa and the Rhone Basin and in locally sandy condensed chamosite oolites of the Spinatum zone in Northamptonshire, Oxfordshire and Somerset (fauna p. 76) in which *Ps. (Ps.) equivalvis* is a relatively rare species compared to similar contemporaneous deposits further north. The maximum height of *Ps. (Ps.) veyrasensis* in the English occurrences is 24.5 mm (SM J40211) but an isolated specimen from the U. Pliensbachian of Normandy has a height of 74.5 mm (GPIG). Other than where indicated above *Ps. (Ps.) veyrasensis* is a rare species. The limited available data suggests that it is more common in the southern parts of its geographic range.

8. INTERPRETATION OF ECOLOGY

Ps. (Ps.) veyrasensis occurs in much the same sedimentary and faunal associations as *Ps. (Ps.) dentatus* thus a similar ecological interpretation can be applied (see p. 76). The fact that the species often co-occur might be adduced to be further evidence for the view (see p. 60) that they in fact constitute polymorphs of the same species. However, the fact that morphs attributable to *Ps. (Ps.) veyrasensis* are unknown after the U. Pliensbachian while those attributable to *Ps. (Ps.) dentatus* are found in the M. Jurassic is difficult to interpret on this basis. Nevertheless the subtle ecological difference which presumably prevents inter-specific competition remains to be demonstrated.

9. FUNCTIONAL MORPHOLOGY

Since *Ps. (Ps.) veyrasensis* is identical to *Ps. (Ps.) dentatus* in almost all aspects of morphology a similar mode of life can be inferred (see pp. 76, 77). Whether they are considered as polymorphs or separate species, a functional explanation for the difference in number of plicae in the two forms is difficult to envisage. Any saving in weight leading to improved swimming ability through the lower number of plicae in *Ps. (Ps.) veyrasensis* would have been offset by the reduced shell strength and stiffness incurred through the longer plical wavelength. It seems more likely that the number of plicae had no functional significance but was controlled by a pleiotropic gene which also coded for a selectively significant physiological difference. Small differences in the mean number of ribs in closely related Recent species of *Cardium* have been accounted for in a similar way (Russell, 1972).

10. ORIGINS AND EVOLUTION

Ps. (Ps.) veyrasensis almost certainly evolved from *Ps. (Ps.) dentatus* but since there is no evidence for heterochrony, speciation presumably involved a major change in the genome. There is a strong suggestion that *Ps. (Ps.) veyrasensis* arose sympatrically in the Rhone basin during the Angulata zone.

The apparent stenotopy of *Ps. (Ps.) veyrasensis* (see Section 8) combined with phyletic increase in height from 27 mm (Hettangian) to 74.5 mm (U. Pliensbachian) indicates the prevalence of 'K' selection for increased trophic efficiency (Gould, 1977).

The post U. Pliensbachian extinction of the species almost certainly relates to the widespread development of unfavourable bituminous shale facies in the L. Toarcian.

Subgenus *ECHINOPECTEN* Brasil 1895

Type species. OD; Brasil 1895, p. 12; *Pecten barbatus* J. Sowerby 1819, p. 53, pl. 231; Aalenian, Normandy.

AMENDED DIAGNOSIS

RV generally flatter than LV and bearing long, depressed spines. Jur. (Toar.-Baj.), Eu., S. Am.

DISCUSSION

Hertlein (1969: N372) contended that *Ps. (Echinopecten)* could be traced back to the Hettangian. This may be a result of the inclusion of *'Pecten' pollux* d'Orbigny within the subgenus. Although the latter has spines on the right valve, the presence of similar ornament on the left valve is unlike the type species. There is no other evidence to suggest that the species are related and *'P.' pollux* is in fact almost certainly descended from a species of *Chlamys*, within which genus it is therefore included. The stratigraphic range of *Ps. (Echinopecten)* is consequently herein regarded as Toarcian – L. Bajocian.

Pseudopecten (Echinopecten) barbatus (J. Sowerby 1819)

Pl. 2, Figs. 15–18; text figs. 64–66

Synonymy

1819	*Pecten barbatus* sp. nov; J. Sowerby, p. 53, pl. 231.
? 1833	*Pecten barbatus* J. Sowerby; Goldfuss, p. 48, pl. 90, fig. 11.
1850	*Pecten barbatus* J. Sowerby; d'Orbigny, v. 1, p. 284.
v* 1850	*Pecten erebus* sp. nov; d'Orbigny, v. 1, p. 284 (Boule, 1910, v. 4, p. 68).
1858	*Pecten barbatus* J. Sowerby; Oppel, p. 420.
1867	*Pecten barbatus* J. Sowerby; Waagen, p. 631.
1868	*Pecten Coquandi* sp. nov. Jaubert, p. 235.
1874	*Pecten barbatus* J. Sowerby; Dumortier, p. 199, pl. 44, fig. 6, p. 310, pl. 42, fig. 5.
1886d	*Pecten limpus* sp. nov; De Gregorio, p. 21, pl. 13, fig. 7.
1886	*Pecten barbatus* J. Sowerby; Rothpletz, p. 36.
1893	*Pecten* cfr. *barbatus* J. Sowerby; Botto-Micca, p. 174.
1895	*Pecten (Echinopecten) barbatus* J. Sowerby; Brasil, p. 12.
1899	*Pecten barbatus* J. Sowerby; Greppin, p. 120, pl. 12, fig. 5.
1911	*Pecten erebus* d'Orbigny; Rollier, p. 266.
1916	*Aequipecten barbatus* (J. Sowerby); Richardson, pp. 473, 497, 498, 513, 515.
1917	*Aequipecten barbatus* (J. Sowerby); Paris and Richardson, p. 521.
1927	*Aequipecten barbatus* (J. Sowerby); Richardson, pp. 53, 57.
1929	*Pecten (Aequipecten) barbatus* J. Sowerby; Lanquine, pp. 199, 300.
1936	*Aequipecten barbatus* (J. Sowerby); Dechaseaux, p. 58.
1950	*Chlamys (Aequipecten) barbata* (J. Sowerby); Channon, p. 247.

Lectotype of *Pecten barbatus* J. Sowerby 1819, p. 53, pl. 231 herein designated; BCM C 2281.1 (the specimen depicted in the lower two figures of J. Sowerby's pl. 231); Inferior Oolite (Aalenian/Bajocian/pars Bathonian), England (see p. 81). Paralectotype; BCM C 2281.2 (the specimen depicted in the upper figure of Sowerby's pl. 231); also Inferior Oolite, England.

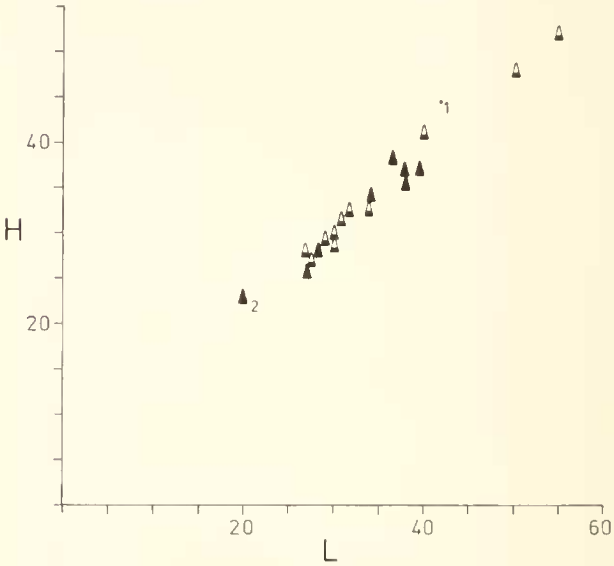
1. ORIGINAL DIAGNOSIS AND DESCRIPTION

'Orbicular, depressed, transversely striated; rays 14, those upon one valve spinose; spines long, acute, depressed; ears nearly equal.

The spinose valve is the flattest; the striae upon it are sharp, and much elevated upon the sides of the rays, from whence they curve into the bases of the spines, of which there are about 5 to each ray. The rays upon the other valve are convex, equal in width to the space between them, and crossed by less elevated striae than those upon the spinose valve. The sides of both valves, near the ears, are perpendicular and neatly pectinated.'

2. AMENDED DIAGNOSIS

Distinguished from all other species of *Pseudopecten* by the presence of long spines on the right valve.



Text fig. 64: *Pseudopecten (Echinopecten) barbatus* – height/length.

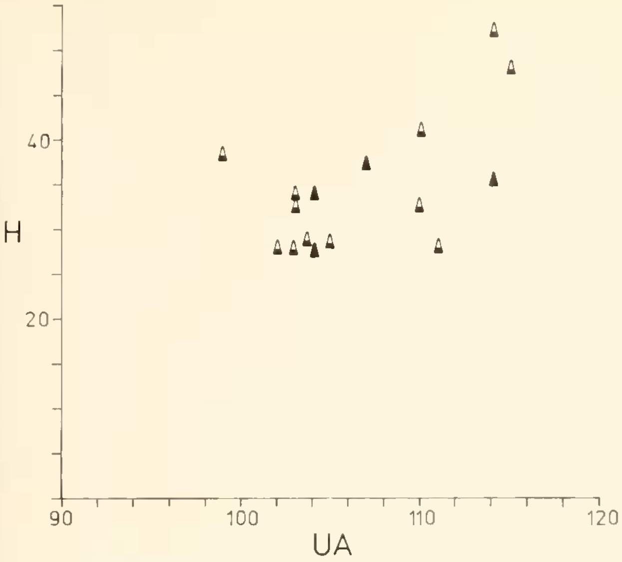
3. AMENDED DESCRIPTION

Disc sub-orbicular in juveniles becoming sub-ovate, longer than high (text fig. 64), near the maximum height of 52 mm (ENSM). Umbonal angle very variable (text fig. 65) but increasing during ontogeny to produce concave dorsal margins. Disc flanks moderately high and ornamented with vertical striae (Pl. 2, Fig. 18).

Equilateral; inequivalve, left valve moderately convex, right valve almost flat.

Intersinal distance greater in left valve than right. Moderately large byssal notch in right valve becoming relatively smaller during ontogeny.

Auricles well demarcated from disc, moderate in size, anterior slightly larger than posterior. Junction with hinge line 90°. Anterior auricle of right valve meeting disc at an acute angle. Posterior auricle of right valve and both auricles of left valve meeting disc at an acute angle. All auricles ornamented with pronounced comarginal striae. Hinge line of right valve bearing dorsally directed spines up to 5 mm in length, spaced at intervals of 2–3 mm (Pl. 2, Fig. 17).



Text fig. 65: *Pseudopecten (Echinopecten) barbatus* – height/umbonal angle.

Exterior of both valves exhibiting 13–14 radial plicae, usually 14 on right valve, 13 on left. Plicae equal in width to sulci, angular on right valve, rounded on left. On left valve both plicae and sulci traversed by comarginal striae (Pl. 2, Fig. 16). On right valve only flanks of plicae bearing comarginal ornament but latter more pronounced than on left valve (Pl. 2, Fig. 17). At shell heights above about 20 mm plicae on right valve also ornamented with ventrally directed spines up to 10 mm in length, usually spaced at intervals of about 5 mm (Pl. 2, Fig. 17).

Plicae rectilinear in form on shell interior. Shell thickness moderate.

4. DISCUSSION

Of the two syntypes of *'Pecten' barbatus* J. SOWERBY in the BCM, the bivalved specimen (C2281.1) is herein selected as lectotype and the other specimen (C2281.2), a right valve seen from the interior, becomes, ipso facto, the paralectotype. The figure of *'P.' barbatus* J. SOWERBY; GOLDFUSS differs markedly from the species described in Section 3 by exhibiting 19 plicae and high H/L and H/UA ratios (1). This may, however, be due to a draughting error and in the absence of the original (apparently destroyed during the 2nd. World War) it is impossible to say whether GOLDFUSS' hypodigm differed from that of J. SOWERBY, and thus whether his use of *'P.' barbatus* should be excluded from the synonymy.

The sole observed syntype of *'P.' erebus* D'ORBIGNY (MNO 2624A; Pl. 2, Fig. 15; 2) from the Bajocian, is a steinkern showing the impression of 14 plicae which are rectilinear in form. In spite of the absence of the diagnostic external spines this feature aligns *'P.' erebus* with *Ps. (Ec.) barbatus* because no other Bajocian pectinids with plicae of this shape and number are known.

No supporting figure was provided in the erection of *'P.' Coquandi* JAUBERT. This species, from the Toarcian of Provence, was said to differ from *'P.' barbatus* by the paucity of spines on some parts of the shell. Since this is a feature of the left valve and early ontogenetic stages of the right valve in J. SOWERBY'S species, JAUBERT'S diagnosis is inadequate. In fact, LANQUINE (1929) has subsequently examined the latter's syntypes and pronounced them to be inseparable from J. SOWERBY'S species.

The figure of *'P.' limpus* DE GREGORIO apparently depicts a specimen of *Ps. (Ec.) barbatus* whose spines have been removed by abrasion.

5. STRATIGRAPHIC RANGE

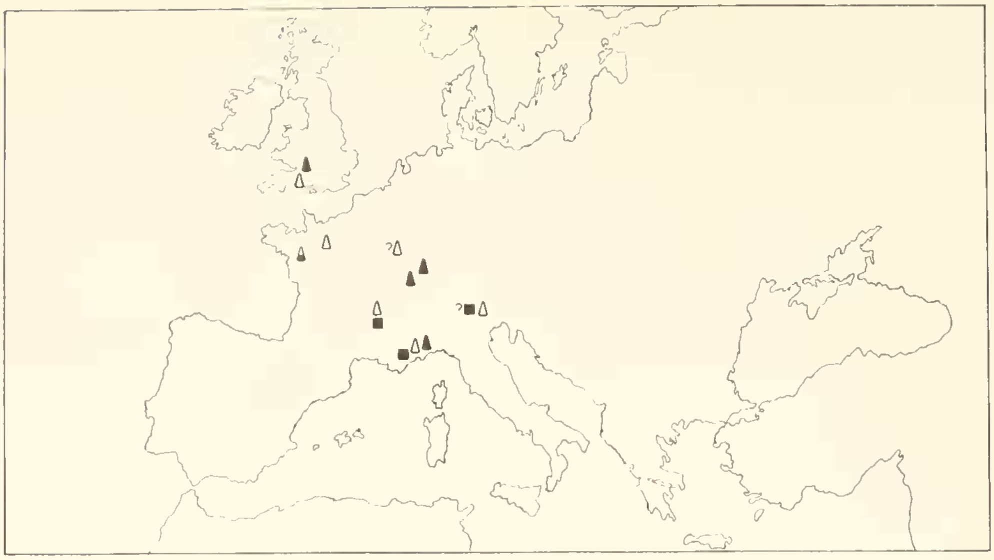
Ps. (Ec.) barbatus first occurs, albeit rather rarely, in the Toarcian of Provence (JAUBERT, 1868; LANQUINE, 1929), the Rhone basin (DUMORTIER, 1874) and possibly N. Italy (DE GREGORIO, 1886d). The earliest records appear to be from the Bifrons zone (L. Toarcian). Subsequently the species becomes locally common in the Aalenian and L. Bajocian. BM 66826, from the Laeviuscula zone, is the latest unequivocal zonally defined record of *Ps. (Ec.) barbatus*. However, PARIS and RICHARDSON (1917) considered that the specimen herein designated as lectotype (see Section 4) was, by the evidence of the matrix, probably derived from the Sauzei zone of Dundry, near Bristol. It may therefore be that some of the many museum specimens labelled 'Inferior Oolite' from this and other localities in S. England are also derived from the Sauzei zone. It seems unlikely that any specimens are derived from later parts of the Bajocian.

6. GEOGRAPHIC RANGE

Ps. (Ec.) barbatus is unknown outside Europe. Within Europe (text fig. 66) its distribution is patchy and largely restricted to S. England and France. This is probably due to the localised development of the appropriate sedimentary facies (see Section 8). There is some evidence for a migration from an initial centre in S. France. Unequivocal Toarcian records are limited to the latter area. Subsequent records from the Opalinum zone of the Aalenian also include specimens from N. Italy (BOTTO-MICCA, 1893) and Dorset (RICHARDSON, 1927). However, *Ps. (Ec.) barbatus* did not spread into northern Europe in numbers until a later date, despite the widespread development of the appropriate sedimentary facies. Thus the Concavum zone marks the first occurrence of numerous specimens in Normandy (BRASIL, 1895) while *Ps. (Ec.) barbatus* did not occur widely in S. England until the Discites zone of the L. Bajocian (PARIS and RICHARDSON, 1917).

7. DESCRIPTION OF ECOLOGY

In the Toarcian and Aalenian of Provence *Ps. (Ec.) barbatus* is found in coarse, occasionally sandy, ferruginous limestones containing chert nodules. Associated faunal elements are predominantly terebratulid and rhynchonellid brachiopods although gastropods and the bivalves *Propeamussium (P.) laeviradiatum*, *Entolium (E.) corneolum*, *Plagiostoma*, *Gervillia*, *Modiolus*, *Gryphaea*, *Astarte*, *Pholadomya* and *Pleuromya* also occur (LANQUINE, 1929). *Ps. (Ec.) barbatus* occurs with a similar fauna (to which is added *P. (P.) pumilum*) in the thin, partly phosphatised, and locally conglomeratic limestones of the Aalenian (Concavum



Text fig. 66: *Pseudopecten (Echinopecten) barbatus* – European distribution.

zone) in Normandy (Brasil, 1895). The species is absent from deposits of the same age in S. Germany which are developed as an expanded shale sequence passing upwards into sandstones and chamosite oolites.

In the Laeviuscula zone (L. Bajocian) of Provence *Ps. (Ec.) barbatus* is quite common and occurs with a fauna similar to that described above (with the addition of *Ctenostreon*) in hard ferruginous limestones. The fossils are heavily corroded and phosphate coated, particularly at a hardground horizon where glauconite and limonite mineralisation has also taken place (Lanquine, 1929). Deposits of similar age in S. England (Discites-Sauzei zones) are developed as condensed ironshot sandy limestones locally containing exogenous limestone pebbles. *Ps. (Ec.) barbatus* is quite common and *P. (P.) laeviradiatum* is a frequent associate in a fauna much the same as that from Provence (Richardson, 1916). Contemporaneous deposits in S. Germany consist of condensed marly oolites from which *Ps. (Ec.) barbatus* has yet to be recorded. The species is also absent from the deep water pelagic limestones of the peri-Mediterranean region. The only records from the latter area are from Provence (see above) and the Aalenian of the Italian Alps (De Gregorio, 1886d; Botto-Micca, 1893) where a few specimens have been found in condensed deposits, probably formed on a submarine rise (fauna p. 31). The few other records of *Ps. (Ec.) barbatus* appear also to be from condensed facies.

8. INTERPRETATION OF ECOLOGY

Ps. (Ec.) barbatus frequently occurs with the stenotopic pectinid *Propeamussium (P.) laeviradiatum* and reference should be made to the analysis presented for this species (p. 31) for a complementary and more detailed interpretation of synecology.

The coarse-grained, condensed deposits in which *Ps. (Ec.) barbatus* usually occurs are indicative of high energy conditions with a low sediment input. Corroded fossils and local non-sequences provide evidence of active erosion, perhaps as a result of storms. The extensive mineralisation associated with slow deposition probably led to the formation of a firm substrate and may also have promoted the local development of hardgrounds.

The associated benthic fauna is characterised by adaptations for stability in the face of high environmental energy. The adaptations of the epifauna are discussed on p. 31. Less common infaunal elements are characteristically deep burrowing bivalves (*Pleuromya, Pholadomya*) which were probably able to avoid the risk of exhumination by living below the base of storm erosion. Genera which probably lived semi-infaunally (*Plagiostoma, Gervillia, Modiolus*) can be adduced, by analogy with Recent analogues (Stanley, 1970), to have attained stability by virtue of a strong byssus.

The absence of *Ps. (Ec.) barbatus* from condensed oolites, such as are developed in the Aalenian and Bajocian of S. Germany, is probably because the shifting nature of such sediments created an unfavourable environment. The development of spinose ornament on the right valve was probably made at the expense of swimming ability (see Section 9), thus occupation of a mobile substrate would have rendered *Ps. (Ec.) barbatus* extremely susceptible to sediment swamping. Moreover, loose ooliths would have probably afforded a poor anchorage for the spines. Deep water pelagic limestones were probably unfavourable to *Ps. (Ec.) barbatus* as a consequence of their soupy nature at the time of deposition, leading to the danger of sediment swamping. The absence of *Ps. (Ec.) barbatus* from expanded coarse-grained sequences (as in the Aalenian of S. Germany) indicates that the favourability of condensed coarse-grained sediments for the species lay in their low turbidity rather than high energy depositional environment.

The usual occurrence of *Ps. (Ec.) barbatus* in only moderate numbers with a high diversity fauna suggest that it was an equilibrium species (Levinton, 1970).

9. FUNCTIONAL MORPHOLOGY

The following features are paradigmatic for a bivalve living in a high energy environment with a reclining habit when adult.

1. Large adult size
2. Thick shell
3. Strongly ornamented lower valve
4. Smooth upper valve
5. Low convexity

Of these, *Ps. (Ec.) barbatus* exhibits features 3, 4 and, to some extent, 5. The strongly spinose and comarginally striated right valve represents, in bioeconomic terms, an efficient means of gripping the substrate in the high energy environments occupied by the species. Presumably environmental energy was never so high as to also necessitate the development of a large thick shell for stability whilst reclining.

The possibility that the spines might represent a 'snow-shoe' adaptation such as has been suggested for *Spondylus* in the Chalk by Carter (1972) can be ruled out because the substrates occupied by *Ps. (Ec.) barbatus* were almost certainly firm (see Section 8). Furthermore the relatively small size of the spines would have tended to localise rather than spread the weight of the shell. In fact P. Woodroof (pers. comm., 1977) reports that *Spondylus* is more common in the Cretaceous in coarse grained firmground deposits rather than the typical Chalk lithology which is indicative of a soupy substrate at the time of deposition.

The moderately large juvenile byssal notch indicates that stability was attained through byssal fixation early in ontogeny. Spines are absent in the juvenile and the size at which these are first secreted (H: 20) may correspond to that at which current-generated overturning moments became too great for a byssus to be profitably employed.

Although the development of both dorsally directed spines on the hinge and ventrally directed spines on the disc must have been highly effective in providing stability against currents from a wide variety of directions, it must also have severely impaired swimming ability, such as might have been required to escape potential predators or sediment swamping (see Section 8). Any attempt to move dorsally (the 'escape response') or ventrally (normal swimming) would have lodged one or other set of spines even more firmly into the sediment and thus prevented 'take-off'. Moreover, even if the animal was able to rise from the sea-floor the spines would have still inhibited swimming by greatly increasing the frictional drag. Ontogenetic increase in umbonal angle indicates an attempt to prolong swimming ability beyond the juvenile stage. However, it seems likely that late in ontogeny attempted predation was resisted by a 'siege' policy to which the well developed plicae contributed by increasing the strength and stiffness of the shell.

10. ORIGINS AND EVOLUTION

The most likely ancestor for *Ps. (Ec.) barbatus* is *Ps. (Ps.) veyrasensis*. The only major difference between the species is the existence of spines on the right valve in the former. There is however no evidence in the form of ancestral allometry to suggest that the appearance of spines could have been due to the relatively simple process of heterochrony and transspecific evolution may therefore have involved a major change in the genome. There is a gap of three zones between the first and last respective appearances of the species and this suggests that speciation took place outside the main range of the ancestor (Europe) in accordance with the allopatric model.

No phyletic trends are apparent in *Ps. (Ec.) barbatus* although a rigorous assessment of the possibility of size change is precluded by the imprecise stratigraphic localisation of most museum specimens. The largest specimen (H: 52, ENSM) is labelled 'Inferior Oolite' (Aalenian/Bajocian).

The post-Sauzei zone extinction of *Ps. (Ec.) barbatus* has no convincing deterministic explanation. Locally, as in the L. Bajocian of Provence, its disappearance is correlated with the onset of unfavourable marl deposition. However, at least in Britain, apparently suitable condensed facies persist into the U. Bajocian, where *Ps. (Ec.) barbatus* is unknown.

Genus *SPONDYLOPECTEN* Roeder 1882

Type species. M; Roeder 1882, p. 52; *Pecten* cf. *erinaceus* Buvignier; Roeder 1882, p. 52, pl. 2, figs. 4a–c; Oxfordian, Alsace.

AMENDED DIAGNOSIS

Sculptured with number of strong, usually rounded, radial plicae, spinose in some species; byssal notch deep; cardinal area of RV with narrow median groove (similar to *Spondylus*) which continues to ligamental pit; hinge of RV with 2 prominent thick teeth which fit into corresponding sockets in LV. (Apparently some species are attached to tip of RV.) Jur. (Aalen. [?Hettang.]-Tithon.), Eu., Afr., Asia.

DISCUSSION

In his diagnosis Hertlein (1969: N364–365) stated that spines were restricted to the left valve in *Spondylopecten*. All the species here described seem to have had spines on both the left and right valves. Hertlein considered that the genus was restricted to reefs but the results of work presented herein suggest that this was not so. The stratigraphic and geographic range given by Hertlein is also extended herein.

Within the toothed Jurassic pectinids two distinct subgroups may be recognised. One has numerous rounded plicae bearing 2–4 rows of spines while the other has fewer, more angular plicae bearing single rows of spines. There is no direct evidence to suggest that one group has evolved from the other and the fact that teeth have been acquired polyphyletically in various Cenozoic '*Chlamys*' species (de Loriol, 1901; Arkell, 1935a) indicates that there are only grounds of convenience for uniting the two groups of toothed Jurassic pectinids within the same genus. They are herein separated at the subgeneric level; the former group being referred to *S. (Spondylopecten)* and the latter to *S. (Pleisiopecten)*. *Plesiopecten* Munier-Chalmas was considered by Hertlein (1969) to be synonymous with *Spondylopecten* Roeder at the generic level. However, apart from the obvious differences in form of the type species (respectively typical and sole species of the two groups delineated above), it has been shown by Arkell (1935a) that Roeder's original conception of *Spondylopecten* did not include the type species of *Plesiopecten* (cf. p. 90). There are thus ample grounds for employing *Spondylopecten* and *Plesiopecten* as separate subgeneric categories.

Subgenus *PLESIOPECTEN* Munier-Chalmas 1887

Type species. M; Munier-Chalmas in P. Fischer 1887, p. 994; *Pectinites subspinosus* Schlotheim 1820, p. 223; U. Jurassic, S. Germany.

AMENDED DIAGNOSIS

Spondylopecten with angular plicae bearing only one row of spines. Jur. (Aalen. [?Hettang.] – Tithon.), Eu., Afr., Asia.

DISCUSSION

Hertlein (1969) did not recognise *Plesiopecten* as a discrete entity and therefore provided no diagnosis.

Jurassic representatives of *S. (Plesiopecten)* cannot be subdivided so all are herein referred to one species, *S. (Pl.) subspinosus*.

Spondylopecten (Plesiopecten) subspinosus (Schlotheim 1820)

Pl. 3, Figs. 1–5, 7, ?Fig. 6; text figs. 67–72.

Synonymy

v* 1820 *Pectinites subspinosus* sp. nov; Schlotheim, p. 223.
? 1833 *Pecten novemplicatus* sp. nov; Münster in Goldfuss, p. 45, pl. 100, fig. 3.
v 1833 *Pecten subspinosus* Schlotheim; Goldfuss, p. 46, pl. 100, fig. 4.
(?) 1850 *Pecten novemplicatus* Münster; d'Orbigny, v. 1, p. 257.
v* 1850 *Pecten Hedonia* sp. nov; d'Orbigny, v. 1, p. 284 (Boule, 1910, v. 5, p. 68, 1909, v. 4, pl. 20, figs. 15–17).
v* 1850 *Lima Bellula* sp. nov; d'Orbigny, v. 1, p. 371 (Boule, 1927, v. 16, p. 130, 1928, v. 17, pl. 6, fig. 1).
1850 *Pecten subspinosus* Schlotheim; d'Orbigny, v. 1, p. 373.
v* 1850 *Pecten Orontes* sp. nov; d'Orbigny, v. 1, p. 373 (Boule, 1927, v. 16, p. 131, 1928, v. 17, pl. 6, figs. 3, 4).
1852 *Pecten subspinosus* Schlotheim; Quenstedt, p. 507, pl. 40, fig. 44.
? 1855 *Pecten aequiplicatus* sp. nov; Terquem, p. 323, pl. 23, fig. 5.
1858 *Pecten Bouchardi* sp. nov; Oppel, p. 492.
v 1858 *Pecten subspinosus* Schlotheim; Quenstedt, p. 500, pl. 67, figs. 3, 4, p. 754, pl. 92, figs. 5, 6.
1862 *Pecten subspinosus* Schlotheim; Thurmann and Étallon, p. 251, pl. 35, fig. 4.
? 1862 *Pecten Sarmerensis* sp. nov; Étallon in Thurmann and Étallon, p. 259, pl. 36, fig. 11.
1863 *Pecten subspinosus* Schlotheim; Lycett, p. 113, pl. 40, fig. 14.
(?) *1865* *Pecten aequiplicatus* Terquem; Terquem and Piette, p. 102.
1867 *Pecten subspinosus* Schlotheim; Laube, p. 10.
? 1878 *Pecten lottii* sp. nov; Gemmellaro and Di Blasi in Gemmellaro, p. 389, pl. 20, figs. 1, 2.
1878 *Pecten Oromedon* sp. nov; de Loriol, p. 160, pl. 22, fig. 21.
v 1883 *Pecten subspinosus* Schlotheim; Boehm, p. 612, pl. 67, figs. 40, 41.
1888 *Pecten Bouchardi* Oppel; Schlippe, p. 134, pl. 2, fig. 13.
1893 *Chlamys subspinosus* (Schlotheim); Siemiradzki, p. 118.
1894 *Pecten subspinosus* Schlotheim; de Loriol, p. 42.
1901 *Pecten (Plesiopecten) subspinosus* Schlotheim; de Loriol, p. 105.
1903 *Pecten subspinosus* Schlotheim; Remes, p. 203.
non 1904 *Chlamys* cf. *aequiplicata* (Terquem); Cossmann, p. 503, pl. 16, fig. 15.
1904 *Pecten (Plesiopecten) subspinosus* Schlotheim; de Loriol, p. 230, pl. 23, figs. 5, 6.
1905 *Pecten subspinosus* Schlotheim; Peron, p. 215.
1905 *Pecten lykosensis* sp. nov; Krumbeck, p. 103, pl. 4, figs. 1a–c.
1905 *Pecten (Chlamys) oromedon* de Loriol; Kilian and Guebhard, p. 817.
1910 *Pecten subspinosus* Schlotheim; Simionescu, p. 13, pl. 2, fig. 13.
1910 *Plesiopecten subspinosus* (Schlotheim); Lissajous, p. 362, pl. 9, fig. 20.
1910 *Chlamys (Aequipecten) Hedonia* (d'Orbigny); Cossmann, p. 12, pl. 1, figs. 14–17.
1912 *Chlamys (Aequipecten) Bouillerieri* sp. nov; Cossmann, p. 2, pl. 1, figs. 5, 6.
1916 *Pecten (Plesiopecten) subspinosus* Schlotheim; Douvillé, p. 74, pl. 9, figs. 6, 6a.
1916 *Aequipecten bouchardi* (Oppel); Richardson, pp. 494, 505, 507, 508, 511.
1916 *Aequipecten bouchardi* (Oppel); Paris and Richardson, p. 522.
1920 *Pecten subspinosus* Schlotheim; Faure-Marguerit, p. 56.
1923 *Plesiopecten fusciacensis* sp. nov; Lissajous, p. 163, pl. 30, figs. 7, 7a, 8, 9.
1926 *Spondylopecten subspinosus* (Schlotheim); Staesche, p. 107, pl. 4, fig. 9.
v 1926 *Spondylopecten Bouchardi* (Oppel); Staesche, p. 108, pl. 4, fig. 8.
1929 *Aequipecten Bouchardi* (Oppel); Lanquine, p. 323.
1931 *Pecten subspinosus* Schlotheim; Yin, p. 122.
1932 *Spondylopecten subspinosus* (Schlotheim); Frentzen, p. 56.
1935a *Plesiopecten subspinosus* (Schlotheim); Arkell, p. 364, pl. 53, figs. 4, 5.
? 1936 *Aequipecten aequiplicatus* (Terquem); Dechaseaux, p. 41.
1936 *Spondylopecten Hedonia* (d'Orbigny); Dechaseaux, p. 65.
1936 *Spondylopecten Bouchardi* (Oppel); Dechaseaux, p. 65.
v 1936 *Spondylopecten subspinosus* (Schlotheim); Dechaseaux, p. 66, pl. 8, fig. 9.
1938 *Plesiopecten subspinosus* (Schlotheim); Weir, p. 50, pl. 3, fig. 18.
1952 *Chlamys (Plesiopecten) subspinosa* (Schlotheim); Cox, p. 18, pl. 1, figs. 9–12.
1964 *Plesiopecten bouchardi* (Oppel); Wellnhofer, p. 39, pl. 1, fig. 27.
? 1973 *Chlamys (Aequipecten) aequiplicata* (Terquem); Lentini, p. 27, pl. 15, fig. 3.
v 1975 *Spondylopecten subspinosus* (Schlotheim); Yamani, p. 59, pl. 3, figs. 3–6.

Lectotype of *Pectinites subspinosus* Schlotheim 1820, p. 223 designated herein; HM MB-M. 25.4; Pl. 3, Fig. 1 herein; H: 13.5, L: 13.5, UA: 90, PL: 12; Hornstein (?Kimmeridgian), Grumbach bei Amberg (Franconia). Paralectotypes; HM MB-M. 25.1–3,5–7 (6 specimens).

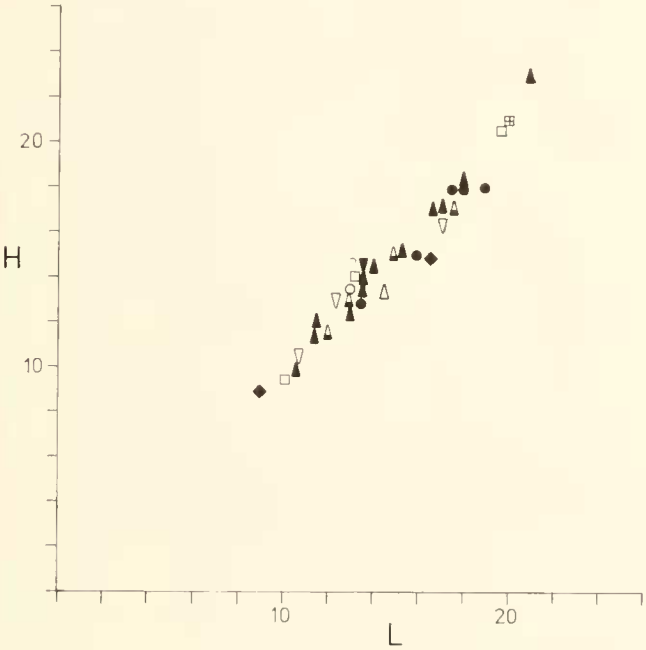
1. ORIGINAL DIAGNOSIS AND DESCRIPTION

‚Mehrere Exemplare in Hornstein, gleichfalls von Amberg (12 Ex.).

In der Form dem vorhergehenden ziemlich ähnlich nur viel kleiner, und höchstens nur einen Zoll im Durchmesser erreichend, mit verhältnismäßig ziemlich breiten, mit gekörnten Querstrichen versehenen Ohren. Von flacherer Wölbung als der vorhergehende. Beyde Hälften gleichförmig gewölbt, die Rippen stark hervorspringend, spitzwinklich zulaufend, und mit kleinen Dornen besetzt. Die sehr feinen eng zusammen stehenden erhabenen Querrippen sind nur in den Zwischenfurchen sichtbar, und veranlassen, daß man Einkerbungen oder vertiefte Punkte in den Zwischenfurchen wahrzunehmen glaubt. Ein darunter befindliches zum Theil verkieseltes Exemplar ist unter den Hornsteinversteinerungen merkwürdig. Er scheint in der dortigen Gegend ziemlich häufig zum Vorschein zu kommen.‘

2. AMENDED DIAGNOSIS

As for diagnosis of subgenus (p. 84).



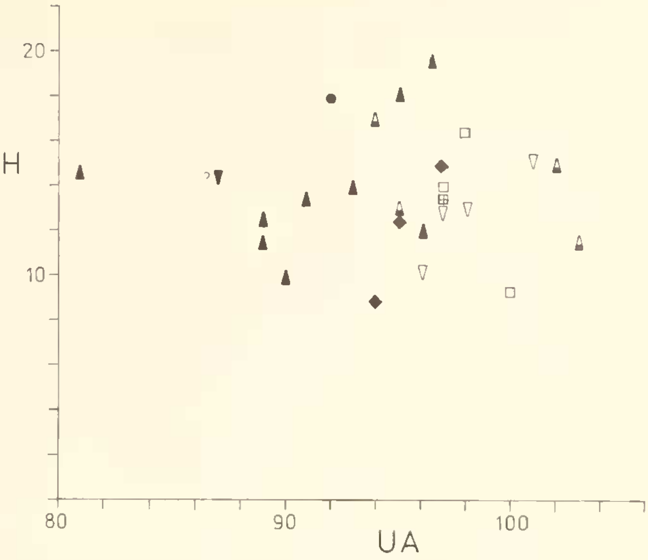
Text fig. 67: *Spondylopecten (Plesiopecten) subspinosus* – height/length.

3. AMENDED DESCRIPTION

Disc sub-orbicular at all ontogenetic stages (text fig. 67), maximum height 27 mm (BM L68240). Umbonal angle very variable (text fig. 68) but increasing slowly during ontogeny to produce slightly concave dorsal margins. Disc flanks high.

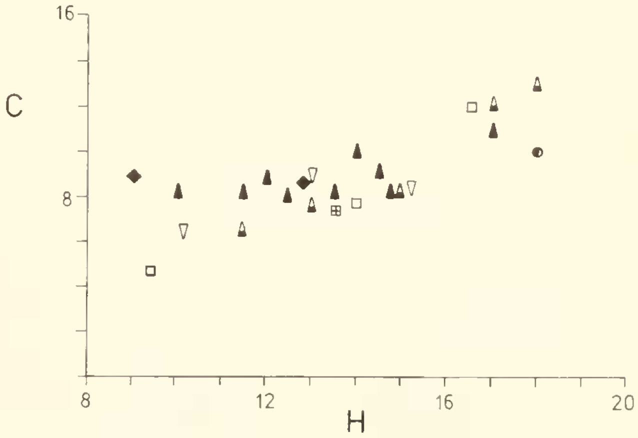
Equilateral, umbones projecting slightly beyond hinge line; equivalve, convexity variable, moderate to high, increasing with approximate isometry (text fig. 69).

Intersinal distance greater in left valve than right. Moderate byssal notch in right valve becoming relatively smaller during ontogeny.



Text fig. 68: *Spondylopecten (Plesiopecten) subspinosus* – height/umbonal angle.

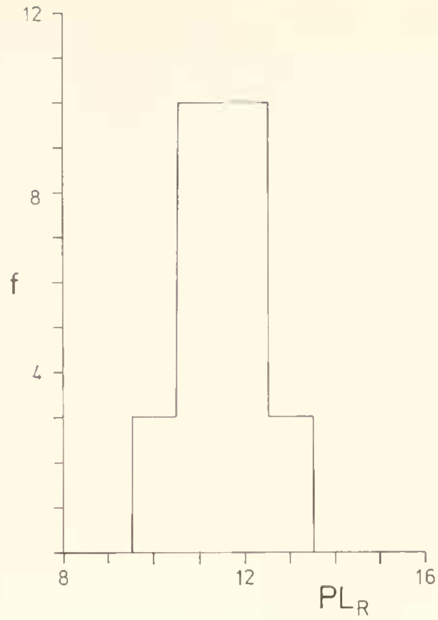
Auricles well separated from disc, moderate in size, anterior larger than posterior. Anterior auricle of right valve meeting hinge line and disc at 90°, anterior auricle of left valve meeting hinge line and disc at an acute angle. Posterior auricles of both valves meeting hinge line and disc at an acute angle. All auricles sloping from umbo towards opposite valve (Pl. 3, Fig. 4) at a maximum angle of 20°. Anterior auricle of right valve ornamented with four radial costae.



Text fig. 69: *Spondylopecten (Plesiopecten) subspinosus* – convexity/height.

Exterior of both valves ornamented with between 10 and 13 angular radial plicae (text fig. 70), equal in width to sulci; usually one more plica in right valve than left. Plicae poorly defined near anterior and posterior margins. Large specimens may develop additional intercalary plicae (Thurmann and Étallon, 1862; Yin, 1931). Crests of plicae bearing ventrally directed spines up to 2 mm in length and spaced at intervals of about 2 mm (Pl. 3, Fig. 3). Sulci traversed by strong comarginal striae (Pl. 3, Fig. 3) fading out on the plical flanks and towards the ventral margins of large specimens (Pl. 3, Fig. 7). Plical cross-section rectilinear and reduced in amplitude on interior of shell (Pl. 3, Fig. 5); shell thickness high.

Cardinal area of right valve bearing two peg-shaped crura (Pl. 3, Fig. 2), anterior larger than posterior and vertically striated; corresponding sockets in left valve.



Text fig. 70: *Spondylopecten (Plesiopecten) subspinosus* – frequency distribution for number of plicae on right valve.

4. DISCUSSION

The 12 syntypes originally described by Schlotheim (1820) as *'Pectinites' subspinosus* were subsequently added to such that the Schlotheim collection (HM) now contains 18 specimens under this specific name (Dr. J. Helms, pers. comm., 1978). The specimens are variably preserved and it is not certain which constitute the syntypes. However, all appear to be referable to the species described in Section 3 and this fact together with the unambiguousness of the description (see Section 1) can leave little doubt as to Schlotheim's hypodigm. Accordingly one of the 18 specimens (HM MB-M. 25.4; Pl. 3, Fig. 1) is herein designed as lectotype and a further 6 specimens (HM MB-M. 25.1–3, 5–7) are selected as paralectotypes.

The single observed type of *'Lima' Bellula* d'Orbigny (MNO 3737) and the sole observed type of *'P.' Hedonia* d'Orbigny (MNO 2421) with 12 and 13 plicae respectively, together with the two syntypes of *'P.' Orontes* d'Orbigny (MNO 3766) with 11 and 13 plicae, all fall within the range of plical variation in *S. (Pl.) subspinosus* and can be distinguished on no other count. Similarly, *'P.' lykosensis* Krumbeck and *'Chlamys' ('Aequipecten') Bouillerieri* Cossmann, both with 11 plicae, cannot be accorded a specific distinction.

Although the figure of *'P.' aequiplicatus* Terquem shows 15 plicae and is similar to *Pseudopecten (Ps.) veyrasensis* the text specifies 12 plicae and spinose ornament as is characteristic of *S. (Pl.) subspinosus*. Some subsequent applications of Terquem's specific name by authors who may have examined the type material appear to bear out the latter assignation (e. g. Lentini [1973] for forms with 10 plicae and Dechaseaux [1936] for forms with 12 plicae and spines). However, Cossmann's (1904) usage is for a form with 16 plicae which is probably referable to *Ps. (Ps.) dentatus* and it is thus conceivable that *'P.' aequiplicatus* Terquem could represent the extremes of variation in the latter species. Unfortunately discussion of the taxonomic position of *'P.' aequiplicatus* is hampered by the fact that the presence or absence of the cardinal crura diagnostic of *Spondylopecten* has yet to be demonstrated in either the specimens cited in the bibliographic references above or in museum specimens from comparable horizons (Lias) examined by the author (however see Section 5). For the same reason the taxonomic position of *'P.' novemplicatus* Münster (a species founded on a fragmentary specimen from the Lias which must have originally possessed about 12 plicae) is also uncertain.

'P.' Bouchardi Oppel was originally erected for forms differing from typical *S. (Pl.) subspinosus* only by their greater convexity and stronger plicae. Staesche (1926), in maintaining a specific distinction, added that such forms were also characterised by wider sulci lacking in comarginal ornament but failed to recognise that all four features are correlates of relatively large size, as is clearly illustrated by his figured specimen (H: 20.9). *'Pl.' fusciacensis* Lissajous, erected for large specimens (H_{max}: 27) lacking comarginal ornament in the sulci, is similarly inseparable from *S. (Pl.) subspinosus* and since the development of intercalary plicae appears to be another correlate of large size (Yin, 1931), *'P.' Sarmerensis* Étallon cannot be accorded a specific distinction on this basis.

'P.' Oromedon de Loriol only differs from *S. (Pl.) subspinosus* by its more rounded plicae. This is almost certainly the result of abrasion.

'P.' lottii Gemmellaro and Di Blasi was erected for a single specimen from the L. Lias resembling *S. (Pl.) subspinosus* in its convexity and *Ps. (Ps.) veyrasensis* in its number of plicae (15). Staesche (1926) has suggested that it may represent a transitional form between the two species (but see Section 10).

5. STRATIGRAPHIC RANGE

None of the small Lias pectinids with approximately 12 plicae whose greater convexity and more angular plicae merit a distinction from *Ps. (Ps.) veyrasensis*, is seen from the interior. It is therefore impossible to say whether the cardinal crura diagnostic of *Spondylopecten* are present and thus whether the specimens in fact constitute examples of *S. (Pl.) subspinosus*. Some of the specimens are devoid of shell (e. g. GPIG 868–4; Pl. 3, Fig. 6) but enough with the remnants of plical spines (e. g. BM L30494) exist to suggest strongly that all are referable to *S. (Pl.) subspinosus*. Of these, the earliest specimen is from the Hettangian (GPIG). Bibliographic records of possibly conspecific specimens (see Section 4) also extend back to the Hettangian in the E. Paris Basin (Terquem, 1855; Terquem and Piette, 1865; Dechaseaux, 1936) and the L. Lias in Sicily (Gemmellaro, 1878; Lentini, 1973). However, there can be no doubt that if it exists at all, *S. (Pl.) subspinosus* is a rare species before the M. Jurassic.

Unequivocal Aalenian records are limited to one specimen from the Opalinum zone (BM L41933) and another from the Murchisonae zone (BM unnumbered) of Dorset. However, the species is quite common by the U. Bajocian and in suitable facies (see Section 8) it is found thus in all stages to the U. Tithonian (Boehm, 1883; Remes, 1903; Faure-Marguerit, 1920; Yin, 1931).

Text fig. 71: *Spondylopecten (Plesiopecten) subspinosus* – World distribution (Callovian reconstruction).

6. GEOGRAPHIC RANGE

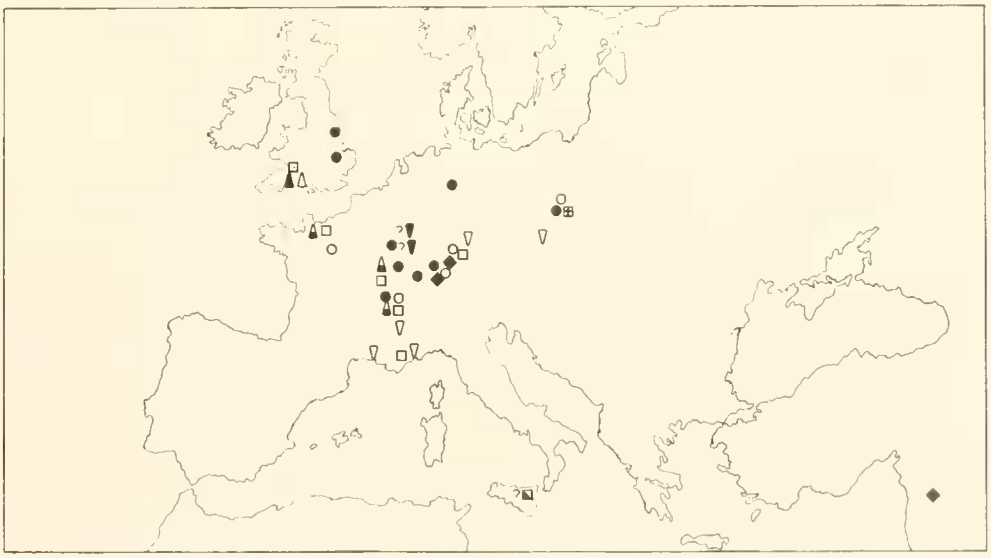
In the M. and U. Jurassic *S. (Pl.) subspinosus* has a geographic range extending south from Europe along the southern shores of Tethys to include about 50° of palaeolatitude (text fig. 71).

Within Europe (text fig. 72) L. Jurassic records are scattered but widespread. However in the M. and U. Jurassic *S. (Pl.) subspinosus* is restricted to those areas which lay north of the Tethyan deep water zone and more locally in the U. Jurassic its numbers are strongly correlated with the development of coral reefs (see Section 8). Nevertheless, only three specimens are recorded by ARKELL (1935a) from apparently suitable coralliferous facies in Cambridgeshire and Yorkshire and this suggests that N. England marked the northern limit of the geographic range of *S. (Pl.) subspinosus*.

7. DESCRIPTION OF ECOLOGY

Potential early records of *S. (Pl.) subspinosus* (see Sections 4, 5) from the Hettangian of Luxembourg (TERQUEM, 1855) and E. France (TERQUEM and PIETTE, 1865; DECHASEAUX, 1936) are derived from sandstones containing abundant gastropods and the bivalves *Cardinia* and *Lima* together with rarer examples of *Chlamys (Ch.) textoria*, *Ch. (Ch.) valoniensis*, *Pseudopecten (Ps.) equivalvis*, *Entolium (E.) lunare* and *Camptonectes (C.) subulatus*.

In the U. Bajocian (Garantiana and Parkinsoni zones) of Somerset and Dorset, *S. (Pl.) subspinosus* occurs quite commonly in brown ferruginous limestones, reaching a maximum height of 23 mm (BM L845528). The associated fauna is abundant and diverse, comprising the bivalves *Pseudomonotis*, *Limatula*, *Trichites*, *Trigonia*, '*Ostrea*', *Pro-*



Text fig. 72: *Spondylopecten (Plesiopecten) subspinosus* – European distribution.

tocardia and a variety of pholadomyoids together with terebratulid brachiopods, in- and epifaunal gastropods, infaunal echinoids and rare corals (RICHARDSON, 1917).

Sediments of Aalenian/Bajocian age in Normandy also contain *S. (Pl.) subspinosus* but the exact horizon and facies is unknown.

Although widespread, the species does not occur commonly anywhere in Europe during the Bathonian. Rare specimens reaching a maximum height of 27 mm are recorded from the Retrocostatum zone (Aspidoides zone of ARKELL, 1956) of the Mâconnais in a condensed ammonite bed (LISSAJOUS, 1923).

S. (Pl.) subspinosus occurs commonly in the condensed ferruginous oolites of the Macrocephalus zone (L. Callovian) in S. Germany and Switzerland (OPPEL, 1858; SCHLIPPE, 1888; STAESCHE, 1926). The maximum size attained is 21 mm (GPIT). Deposits of the same age in Cutch (India) are developed as limestone/shale alternations containing common *S. (Pl.) subspinosus* in association with *S. (S.) palinurus* and the 'coarse' and 'intermediate' phenotypes of *Ch. (Ch.) textoria*. Elsewhere the species is rare in the Callovian but it returns in large numbers in the Oxfordian, particularly to E. France and Switzerland where the stage is frequently developed in reefal facies. *S. (Pl.) subspinosus* is particularly abundant in the U. Oxfordian of the Yonne where, in addition to the framework of corals and *Diceras*, there is an abundant associated fauna including the coral-inhabiting *S. (S.) palinurus, S. (S.) subpunctatus, Camptonectes (C.) virdunensis* and *Radulopecten inequicostatus* together with the 'coarse' phenotype of *Ch. (Ch.) textoria* (PERON, 1905). However, *S. (Pl.) subspinosus* also occurs quite commonly in the L. Oxfordian of the same region which is developed as marls and non-reefal limestones. In similar sediments in the Transversarium zone (U. Oxfordian) of Isere it reaches a height of 27 mm (BM L68420).

S. (Pl.) subspinosus and other species of *Spondylopecten* are absent from the M. and U. Oxfordian reefs of the Oxford area yet coral/*Nerinea*-rich facies at a similar palaeolatitude (text figs. 71, 72) in Poland contain common examples of *S. (Pl.) subspinosus* together with *S. (S.) palinurus, S. (S.) globosus, R. inequicostatus* and *Ch. (Ch.) textoria* (SIEMIRADZKI, 1893).

S. (Pl.) subspinosus is absent from Kimmeridgian coral/*Diceras* facies in the Jura (e. g. CONTEJEAN, 1859) and is likewise absent from coral patch reefs of the same age at La Rochelle (Charente Maritime). Other reef dwelling pectinids are extremely rare at the latter locality although the bivalve fauna is otherwise rich (HALLAM, 1975b).

Tithonian records of *S. (Pl.) subspinosus* are restricted to localised reefal deposits. Thus the species is found in the L. Tithonian of Nattheim (FRENTZEN, 1932) and Neuburg (YAMANI, 1975) in S. Germany; the U. Tithonian of Stramberg in Czechoslovakia (BOEHM, 1883; REMES, 1903), Isère (FAURE-MARGUERIT) and Languedoc (YIN, 1931) in S. France, and also undifferentiated Tithonian in S. France (KILIAN and GUEBHARD, 1905) where it reaches a maximum height of 19 mm. The associated fauna is in all cases rich and diverse and dependant on the locality is made up of various combinations of the reef-dwelling pectinids mentioned above (to which is added *S. (S.) cardinatus)* together with *Plagiostoma, Trichites, Gervillella, Diceras* and *Arctostrea*, pleurotomariid and nerineid gastropods, thick shelled terebratulid brachiopods, cidaroid echinoids, crinoids, corals and calcareous sponges. In what are otherwise faunally indistinguishable facies in the L. Tithonian of Sicily, *S. (Pl.) subspinosus* is absent (GEMMELLARO and DI BLASI, 1874; GEMMELLARO, 1875).

8. INTERPRETATION OF ECOLOGY

Both HERTLEIN (1969) and HALLAM (1976) consider *Spondylopecten* to be an exclusively reef-inhabiting genus. While in the case of *S. (Pl.) subspinosus* it is undoubtedly true that the species occurs most abundantly in reefal deposits, the data of Section 7 provide good evidence that for at least the pre-Tithonian parts of its range *S. (Pl.) subspinosus* was not confined to this habitat. All pre-Oxfordian records appear to be from faunally diverse level bottom situations, usually accompanied by fairly high environmental energy. Such facies also contain the largest representatives of the species. The occasional presence of corals and reef-associated *Chlamys* and *S. (Spondylopecten)* species might be held to indicate that *S. (Pl.) subspinosus* was derived from unexposed reefs nearby. However, more coral-rich horizons (e. g. Upper Coral Bed, U. Bajocian, S. England) containing numerous examples of *S. (Spondylopecten)* are noticeably lacking in *S. (Pl.) subspinosus*. Moreover, undoubted reefs, such as those of the U. Pliensbachian in Morocco (DUBAR, 1948) and the L. Bajocian in E. France (HALLAM, 1975b) were not colonised. In the former case the absence of the reef-associated 'coarse' phenotype of *Ch. (Ch.) textoria (S. (Spondylopecten)* had yet to arise) could indicate that a general competitive exclusion by the common *Pseudopecten, Lithiotis* and *Pachyrisma*, was in operation. However, in the latter case no such process can be invoked as these forms are absent and the 'coarse' phenotype of *Ch. (Ch.) textoria*, a frequent associate of *S. (Pl.) subspinosus* at later horizons, is abundant. Nevertheless, with respect to a general synthesis of habitat range in the Bajocian, it must be admitted that the absence of of *S. (Spondylopecten)* species (which also occur with the 'coarse' phenotype of *Ch. (Ch.) textoria* at later horizons) suggests that some special feature of the L. Bajocian reefs in E. France made them unfavourable to *Spondylopecten* as a whole (see below). Even so, given the foregoing evidence the onus of proof must now pass to those who would still claim that *Spondylopecten* was an entirely reef-restricted genus.

Reefs were first undoubtedly colonised in the Oxfordian although level bottom environments were also inhabited. Subsequently in the Tithonian, reefs apparently became the sole habitat. The diverse fauna of byssate *(S. (Spondylopecten), Ch. (Ch.) textoria, Trichites, Gervillella)* and cemented *(Diceras, Arctostrea)* bivalves attests to the abundance of hard substrates while the luxuriance of the coral growth indicates that the sea was shallow, warm, well oxygenated and of low turbidity.

The absence of *S. (Pl.) subspinosus* from some U. Jurassic reefs within the latitudinal range of the species could perhaps be explained by their particular coral fauna and resultant structure. Personal examination of the in situ L. Kimmeridgian patch reefs near La Rochelle, in which other species of

Spondylopecten are also extremely rare, reveals that they are dominated by sheet and dome-like masses of *Isastrea* and *Thamnasteria* which produce a very dense structure. (The same is true of the L. Bajocian reefs in E. France – see above.) As such they could have provided relatively few sites for the kind of nestling habit inferred for *Spondylopecten* (see Section 9). By contrast, at least in the L. Tithonian reef at Nattheim, there is a dominance of the arborescent *Thecosmilia* (Frentzen, 1932) which could have afforded abundant nestling sites for *S. (Pl.) subspinosus* and the other common species of *Spondylopecten*. In addition to its absence at La Rochelle, *S. (Pl.) subspinosus* is, however, also lacking in the Oxfordian reefs around Oxford and these reefs, apparently within the latitudinal range of *S. (Pl.) subspinosus*, contain abundant *Thecosmilia*. Possibly this apparent anomaly may yet be explained as a consequence of some overriding large-scale control on distribution (e. g. environmental stability – see below). However, the presence of *S. (Spondylopecten)* species and the absence of *S. (Pl.) subspinosus* from the L. Tithonian reefs in Sicily casts further doubt on the importance of general reef structure in determining the occurrence of *Spondylopecten*, and the extreme rarity of *S. (S.) palinurus* at Nattheim also suggests that forms were subject to a more specific control (see p. 96). Unfortunately there are no modern reef-dwelling morphological analogues of *S. (Pl.) subspinosus* to allow a comparison in micro-habitat preference. The pectinid fauna of Recent reefs appears to be dominated by *Chlamys* species of low convexity (Waller, 1972b).

From the foregoing one may reach the speculative conclusion that *S. (Pl.) subspinosus* gradually evolved from being a member of level bottom communities into one confined to the reef habitat and that within the latter there may have been a preference for the more open structures produced by branching corals. Possibly some unpreserved softbodied organism afforded the same niche prior to the occupation of coral reefs since the small convex shell would have been poorly suited to life on the sea floor (see Section 9). The usual occurrence of *S. (Pl.) subspinosus* in moderate numbers in a high diversity fauna suggests that it was an equilibrium species (Levinton, 1970).

The absence of *S. (Pl.) subspinosus* from fine-grained deposits such as the pelagic limestones of the M. & U. Jurassic in the Tethyan region and the phyllosilicate clays of the Oxfordian and Kimmeridgian in N. Europe suggests strongly that the species was intolerant of turbid waters and soupy substrates. While *S. (Pl.) subspinosus* does occur in limestone/shale (Callovian, Cutch) and limestone/marl (L. Oxfordian, Yonne) sequences, it seems highly likely that the species was restricted to relatively coarse-grained limestones.

The rarity of *S. (Pl.) subspinosus* in the Oxfordian coralliferous deposits of central and northern England (see Section 6) may be simply the result of a temperature dependence. However, Hallam (1975a) has proposed a multi-component explanation based on stability theory (Sanders, 1968, 1969) for the N/S provinciality exhibited by a variety of Jurassic taxa and it could thus be that the general environmental instability resulting from shallower seas, greater seasonal fluctuations in temperature and the more frequent incidence of storms caused the relatively stenotopic *S. (Pl.) subspinosus* to be excluded from high latitudes.

9. FUNCTIONAL MORPHOLOGY

The small adult size and relatively large byssal notch of *S. (Pl.) subspinosus* indicate that the species could have remained byssate throughout ontogeny. However, the thick, strongly inflated shell is non-paradigmatic for a free-swinging mode of life and in the absence of any downward slope of the hinge line from posterior to anterior, the high convexity of the right valve renders the species poorly adapted to tight fixation on a single planar surface. Suitably pitted surfaces could have provided nestling sites for the right valve but the similarity in shape and ornament of the valves suggests that both were exposed to the same environment. Thus it is proposed that *S. (Pl.) subspinosus* lived tightly fixed between two or more surfaces with the ventrally directed spines gripping the substrate and adding to the effect of a heavy shell and byssus in providing stability against the actions of currents, waves and predators. Under such circumstances effective fixation could only have been achieved by a close matching of shell convexity to width of 'cavity'. This might have resulted from either of two strategies:

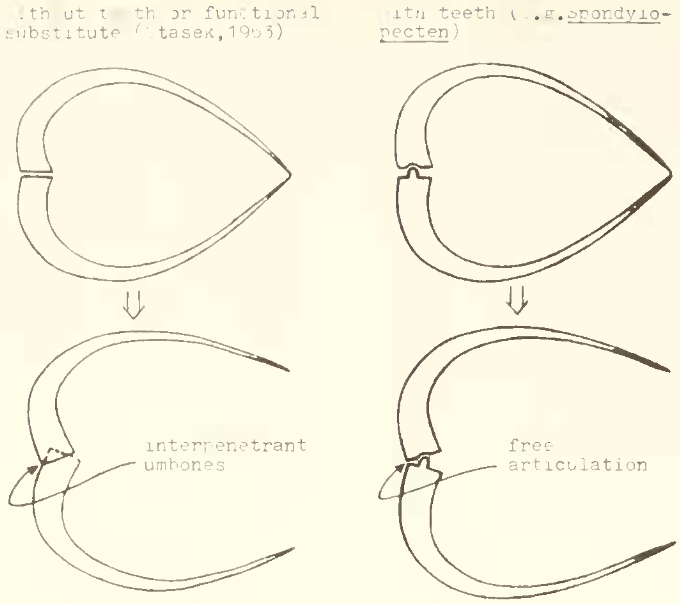
1. Developmental flexibility in convexity to suit the micro-habitat in which the spat initially settled.

2. Selection by the spat of micro-habitats of appropriate size and shape.

Some evidence for the former is provided by the variation in convexity of *S. (Pl.) subspinosus*. However, it cannot yet be said whether this is a positively adaptive trait brought about by developmental flexibility. Some evidence for the latter strategy is provided by the occurrence of *S. (Pl.) subspinosus* with other *Spondylopecten* species, implying that selection of micro-habitats of species-specific size and shape prevented competition for space and thus allowed coexistence. In this respect it is worth noting that of the total of only three features which aid in distinguishing *Spondylopecten* species, one is convexity. Since *Spondylopecten* usually occurs in reefs there is the possibility that the growth forms of different coral species provided the appropriate crevices, fissures etc. for each species of *Spondylopecten* (but see p. 96). For *S. (Pl.) subspinosus* it is likely that some softbodied organism played the same role during the early part of its stratigraphic range (see Section 8).

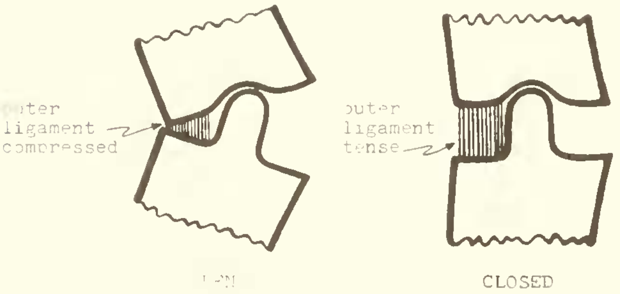
Further evidence for the vital role of convexity in the *Spondylopecten* mode of life is provided by the impressive array of coadaptations which high convexity has necessitated. Departure from the low convexity form of most pectinids raises the problem of interpenetrant umbones when gnomonic growth of the shell results in a logarithmic spiral of more than half a revolution (Stasek, 1963). In the apparent impossibility of interumbonal growth or lateral displacement of the umbones in the Pectinidae, the problem seems to have been solved in *Spondylopecten* by the development of teeth which effectively lift the hinge out of the plane of commisure and thus prevent umbonal friction (text fig. 73). This has the disadvantage of tending to split the ligament upon shell closure (text fig. 74) thus a further adaptation, downward growth of the auricles towards the opposite valve, is required to maintain contact between the valves (Pl. 3, Figs. 4, 8).

In contrast to the above interpretation, Staesche (1926) contended that thickness, convexity, prominent plicae and



Text fig. 73: Articulation in high convexity shells (schematic).

cardinal teeth were all strengthening adaptations to the turbulent environment of a reef. However, STANLEY (1970) has shown that the most exposed of modern shores are colonised by relatively thin-shelled, unornamented bivalves, thereby implying that water movements even of a violent kind are insufficient to warrant the development of a strong shell. Similarly STAESCHE's suggestion that the above features are strengthening adaptations directed against crab predation in the reefal environment can be ruled out because there is no evidence to suggest that this is any more of a problem in reefs than in level-bottom communities, where smooth, flat, thin-shelled, edentulous pectinids also occur.



Text fig. 74: Schematic section of umbonal region in *Spondylopecten* with probable condition of outer ligament upon valve opening and closure.

It is unlikely that the plicae could have added any useful strength and stiffness to that provided by the thick shell and it is more probable that they served to increase purchase upon the substrate (see above).

The heavy shell, moderate to high convexity and prominent ornamentation render it unlikely that *S. (Pl.) subspinosus* could have been anything more than a very inefficient swimmer.

10. ORIGINS AND EVOLUTION

On the basis of its overall similarity, the most likely ancestor for *S. (Pl.) subspinosus* is *Pseudopecten (Ps.) veyrasensis*. The acquisition of cardinal teeth, spinose ornament and a different pattern of plical variation (10–13 cf. 12–15 plicae) by *S. (Pl.) subspinosus* cannot be attributed to heterochrony acting upon ancestral allometries so it is likely that trans-specific evolution involved a profound rearrangement of the genome. STAESCHE (1926) considered that '*Pecten*' *lottii* GEMMELLARO and DI BLASI (see Section 4) represented a transitional stage between *Pseudopecten* and *Spondylopecten*. However, the species is only known from one example (from an unspecified horizon in the L. Lias) thus '*P.*' *lottii* is more reasonably to be thought of as an extreme variant of either *S. (Pl.) subspinosus* or *Ps. (Ps.) veyrasensis* rather than an indicator of gradual evolution between the species.

There appear to be no phyletic changes within *S. (Pl.) subspinosus*. The range of plical variation remains constant; forms with 10 and 13 plicae being known from the M. (e. g. BM 65939 and MNO 2421) and U. (e. g. MNP S3842 and MNO 3766) Jurassic. Apparent phyletic oscillations in maximum height from 23 mm (U. Bajocian) to 27 mm (U. Bathonian) to 21 mm (L. Callovian) to 27 mm (U. Oxfordian) to 19 mm (Tithonian) could well be related to the environment (see Section 8).

Subgenus *SPONDYLOPECTEN* s. s.

(synonym *Cardinopecten* ROLLIER 1904)

ORIGINAL DIAGNOSIS

(see p. 83 for the reason for the inclusion of this section)

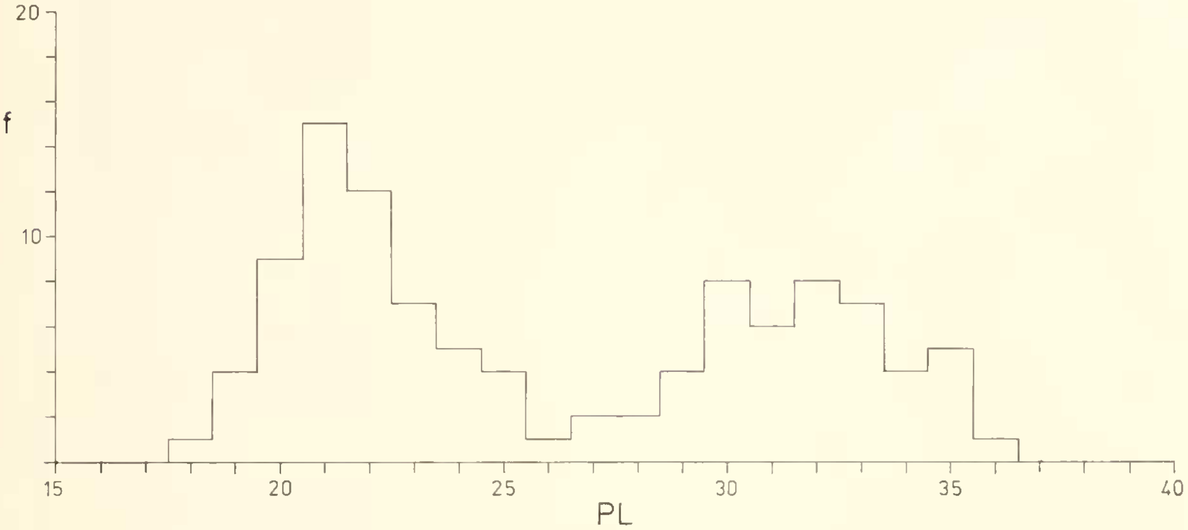
‚Das interessanteste an diesen Formen ist jedenfalls das Schloß, und darüber geben meine verkieselten Exemplare guten Aufschluß. Auf der rechten Klappe sieht man unter dem wenig gewölbten Wirbel eine verhältnismäßig breite Area, die durch die Bandgrube wie bei *Spondylus* gespalten ist.

Neben der Bandgrube liegen unter der Area jederseits Zähne und zwar ist der vordere bedeutend größer, vorausgesetzt, daß der hintere nicht teilweise abgebrochen ist, was bei meinen Exemplaren immerhin möglich wäre.

Quenstedt hebt diese Ungleichheit der Zähne jedoch auch für seinen *Pecten globosus*. . ., auf den ich gleich noch zu sprechen komme, hervor, deshalb scheint sie also normal zu sein. Der große Vorderzahn ist löffelförmig in die Höhe gekrümmt und zeigt auf der Area zugekehrten Seite senkrechte, parallel Streifen; der Hinterzahn ist klein und undeutlich, er erhebt sich kaum über die Area. Außerdem ist der gerade Schloßrand, vorn der Oberrand des Ohres, mit feinen senkrechten Kerben versehen. Von der linken Klappe besitze ich leider kein ganz erhaltenes Schloß; ich habe nur die senkrechten Kerben auf dem Schloßrande constatiren können.' (relevant extract from description of *Pecten (Spondylopecten)* cf. *erinaceus* Buvignier; Roeder, 1882)

AMENDED DIAGNOSIS

Spondylopecten with rounded plicae bearing 2–4 rows of spines. Jur. (Aalen. – U. Tithon.), Eu., Afr., Asia.



Text fig. 75: *Spondylopecten (S.) palinurus/subpunctatus* – frequency distribution for number of plicae.

DISCUSSION

In general form all members of *S. (Spondylopecten)* are very similar. It is possible therefore that the sub-groups identified below could be polymorphs of the same species. However, with the apparent impossibility of detecting polymorphism in the fossil record it seems preferable to treat them as separate species.

In measured museum specimens the range of plical variation in *S. (Spondylopecten)* is from 18–71. Within the range 18–36 plicae there is an essentially bimodal distribution grouped around modes at 21 and 30/32 plicae with an intervening trough at 26 plicae (text fig. 75). Individuals in the former group (herein referred to *S. (S.) palinurus)* also seem to differ from those in the latter (herein referred to *S. (S.) subpunctatus)* by their lower convexity (text figs. 77, 84) and in the possession of four rather than two rows of plical spines. The single known specimen with 26 plicae (MNP) is abraded but apparently originally bore four rows of spines. It is therefore considered to indicate the upper limit of plical variation in the former group.

Within the first group later populations differ in the mode and range of plical variation (text fig. 79) and in convexity (text fig. 77). While there can be little doubt of an ancestor-descendant relationship some authors would consider such differences worthy of a specific separation. However, apart from the difficulties of objectively defining the species there is no evidence that separate lineages existed at any one time. In fact there is some evidence (see p. 97) that earlier and later populations were linked by gradual phyletic evolution. Thus following the rationale adopted in this work, the earlier and later populations are herein considered to belong to the same species. Similar reasoning can be applied to the group of forms referred to *S. (S.) subpunctatus* in which later samples differ in the mode and range of plical variation (text fig. 86) and in convexity (text fig. 84) but in which there is no evidence for coexisting lineages, yet a certain amount for phyletic gradualism (see p. 102).

The paucity of available museum specimens renders it difficult to make any objective division in forms with more plicae than *S. (S.) subpunctatus*. Except where indicated, museum specimens with the following plical counts are only known singly: 42, 43 (3), 44 (3), 45, 46, 48, 51, 52, 53 (2), 54, 56, 60, 63, 64, 71. However, foreign authors who have undoubtedly had access to a greater volume of material provide good evidence for a bimodal distribution in the frequency of plical counts. Staesche (1926) refers to specimens with about 45 plicae while Yin (1931) refers to a number of specimens with between 42 and 48 plicae, thus forms within the latter range are considered to belong to a third *S. (Spondylopecten)* species, *(S. (S.) cardinatus)*. Boehm (1883) records 55 specimens with over 60 plicae while Stafsche (1926) records numerous specimens with between 55 and 65 plicae, thus forms within the latter range, together with rare museum specimens with plical counts just outside this range (51, 52, 53, 54, 71) are considered to belong to a fourth *S. (Spondylopecten)* species *(S. (S.) globosus)*.

Spondylopecten (Spondylopecten) palinurus (d'Orbigny 1850)

Pl. 3, Figs. 8–14; text figs. 75 (pars), 76–81

Synonymy

1850 *Pecten palinurus* sp. nov; d'Orbigny, v. 1, p. 342 (Boule, 1925, v. 14, p. 161, pl. 20, figs. 11, 12).
v* 1850 *Pecten Nireus* sp. nov; d'Orbigny, v. 2, p. 22 (Boule, 1929, v. 18, p. 174, pl. 20, figs. 5, 6).
1850 *Pecten Nicaeus* sp. nov; d'Orbigny, v. 2, p. 22 (Boule, 1929, v. 18, p. 174, pl. 20, figs. 7, 8).
1852 *Pecten erinaceus* sp. nov; Buvignier, p. 23, pl. 19, figs. 7–12.
v* 1857 *Pecten symmetricus* sp. nov; Morris in Hull, p. 103, pl. 1, figs. 3, 3a–c.
1858 *Pecten subpunctatus* Münster; Quenstedt, p. 627, pl. 77, figs. 27–29 (non Münster sp.).
1859 *Pecten Monsbeliardensis* sp. nov; Contejean, p. 316, pl. 23, figs. 16–18.
1860 *Pecten Nicaeus* d'Orbigny; Coquand, p. 79.
1862 *Pecten erinaceus* Buvignier; Thurmann and Étallon, p. 250, pl. 35, fig. 2.
1862 *Pecten araricus* sp. nov; Étallon in Thurmann and Étallon, p. 251, pl. 35, fig. 3.
1862 *Pecten Monsbeliardensis* Contejean; Thurmann and Étallon, p. 252, pl. 35, fig. 5.
? 1874 *Pecten catulloi* sp. nov; Gemmellaro and Di Blasi, p. 107, pl. 2, figs. 1–5.
? 1875 *Pecten catulloi* Gemmellaro and Di Blasi; Gemmellaro, p. 42.
1880 *Pecten semiarticulatus* sp. nov; G. Meneghini, p. 357, pl. 22, fig. 18.
1881 *Pecten cartieri* sp. nov; de Loriol, p. 88, pl. 12, figs. 8–10.
1881 *Pecten erinaceus* Buvignier; de Loriol, p. 92, pl. 13, figs. 1, 2.
1882 *Pecten (Spondylopecten)* cf. *erinaceus* Buvignier; Roeder, p. 52, pl. 2, figs. 4a–c.
1893 *Pecten Cartieri* de Loriol; Siemiradzki, p. 119.
1894 *Pecten erinaceus* Buvignier; de Loriol, p. 48, pl. 5, fig. 4.
? 1897 *Pecten Soybierensis* sp. nov; de Loriol, p. 128, pl. 15, fig. 6.
(?) 1899 *Pecten Soybierensis* de Loriol; de Loriol, p. 170.
? 1900 *Pecten Soybierensis* de Loriol; de Loriol, p. 128.
1901 *Pecten (Chlamys) Roederi* sp. nov; de Loriol, p. 103, pl. 6, figs. 6, 7.
? 1903 *Pecten subpunctatus* Münster; Remes, p. 203, pl. 19, figs. 8a–c (non Münster sp.).
(?) 1904 *Pecten Soybierensis* de Loriol; de Loriol, p. 217.
1904 *Pecten subpunctatus* Münster; de Loriol, p. 217, pl. 23, fig. 4 (non Münster sp.).
1905 *Pecten* sp; Krumbeck, p. 104, pl. 14, figs. 2a–d.
v 1905 *Pecten erinaceus* Buvignier; Peron, p. 214, pl. 10, fig. 1.
1907a *Chlamys Grossouvrei* sp. nov; Cossmann, p. 239, pl. 8, fig. 19.
? 1910 *Pecten subpunctatus* Münster; Simionescu, p. 14 (non Münster sp.).
1912 *Chlamys (Aequipecten) palinurus* (d'Orbigny); Cossmann, p. 2, pl. 1, figs. 1–4.
1912 *Pecten semiarticulatus* G. Meneghini; Dal Piaz, p. 246, pl. 1, figs. 15a, 15b.
v 1916 *Aequipecten symmetricus* (Morris); Paris and Richardson, p. 523, pl. 44, figs. 6a, 6b.
1925 *Chlamys (Aequipecten) syriacus* sp. nov; Cossmann in Douvillé and Cossmann, p. 325, pl. 8, figs. 7a–c.
1926 *Chlamys erinaceus* (Buvignier); Roman, p. 196.
? 1931 *Pecten (Spondylopecten) erinaceus* Buvignier; Yin, p. 119.
v*? 1935a *Chlamys (Aequipecten) macfadyeni* sp. nov; Cox, p. 176, pl. 23, figs. 11a, 11b.
1936 *Spondylopecten erinaceus* (Buvignier); Dechaseaux, p. 67.
1952 *Chlamys (Spondylopecten) stoliczkai* sp. nov; Cox, p. 15, pl. 3, figs. 14–20.
v* 1952 *Chlamys (Spondylopecten?) badiensis* sp. nov; Cox, p. 16, pl. 1, figs. 14a, 14b.
1958 *Chlamys (Aequipecten)* cf. *palinurus* (d'Orbigny); R. Hudson, p. 419.
(?) *1958* *Chlamys (Aequipecten) syriaca* Cossmann; R. Hudson, pp. 419, 420.
? 1959 *Aequipecten kotsubu* Kimura; Tamura, p. 58, pl. 6, figs. 33, 34.
v 1964 *Spondylopecten grossouvrei* (Cossmann); J.-C. Fischer, p. 18, pl. 1, figs. 11, 12.
1965 *Chlamys (Spondylopecten) badiensis* Cox; Cox, p. 58, pl. 7, figs. 3, 4.

Lectotype of *Pecten palinurus* d'Orbigny 1850, v. 1, p. 342 designated herein; MNO 3401; figured Boule, 1925, pl. 20, figs. 11, 12; Callovian, Pizieux (Sarthe). Paralectotype; also MNO 3401; Callovian, Etrochey (Côte d'Or).

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

'Espece renflée, presque ronde à 20 côtes regulières, aplaties, plus larges que les sillons, avec des indices de dents sur les côtes. France, Pizieux'.

2. AMENDED DIAGNOSIS

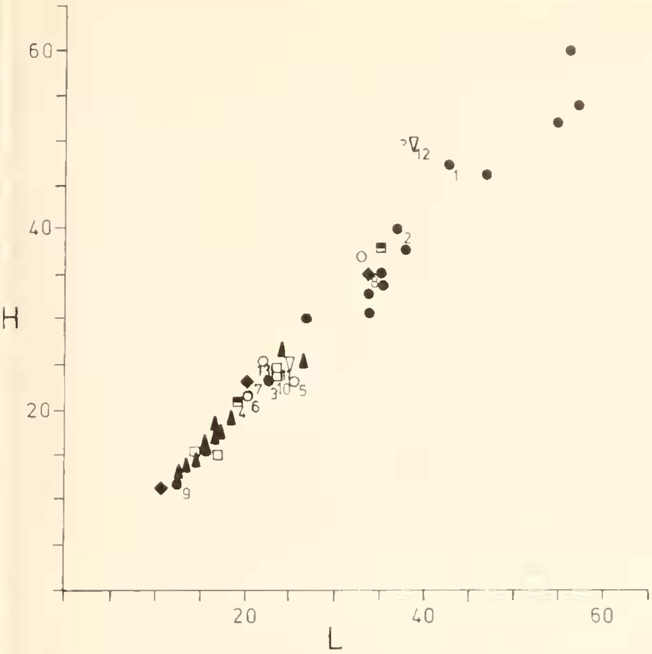
Distinguished from all other species of *S. (Spondylopecten)* by the number of plicae (26 or less).

3. AMENDED DESCRIPTION

Disc sub-orbicular at all sizes (text fig. 76), maximum height 62 mm (de Loriol, 1894). Umbonal angle very variable (text fig. 78) but increasing (at a decreasing rate) during ontogeny to produce concave dorsal margins. Disc flanks moderately high.

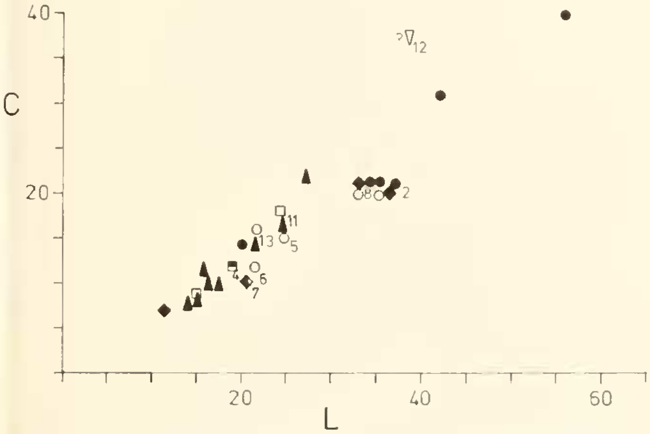
Equilateral; equivalve, convexity variable, moderate to high, apparently increasing allometrically at a faster rate in earlier representatives (text fig. 77).

Intersinal distance greater in left valve than right; moderately large juvenile byssal notch becoming relatively smaller during ontogeny.



Text fig. 76: *Spondylopecten (S.) palinurus* – height/length.

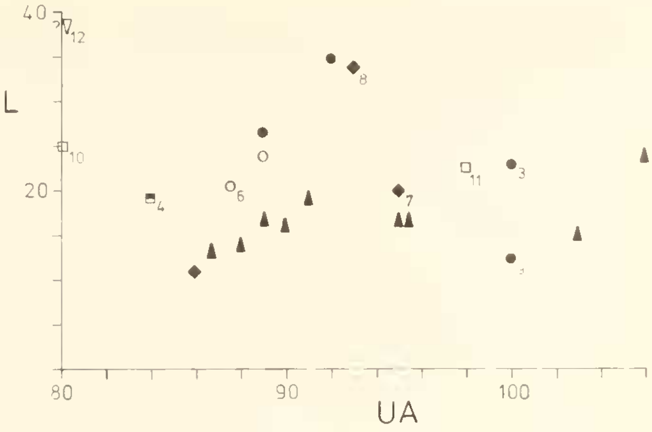
Auricles well demarcated from disc, moderate in size, anterior larger than posterior. Anterior auricles meeting hinge line at about 90°, posterior auricles meeting hinge line at an obtuse angle. Right anterior auricle meeting disc at an obtuse angle; remaining auricles meeting disc at an acute angle. Right anterior auricle bearing between 5 and 8 radial costae. All auricles sloping downwards from umbo towards opposite valve (Pl. 3, Fig. 8).



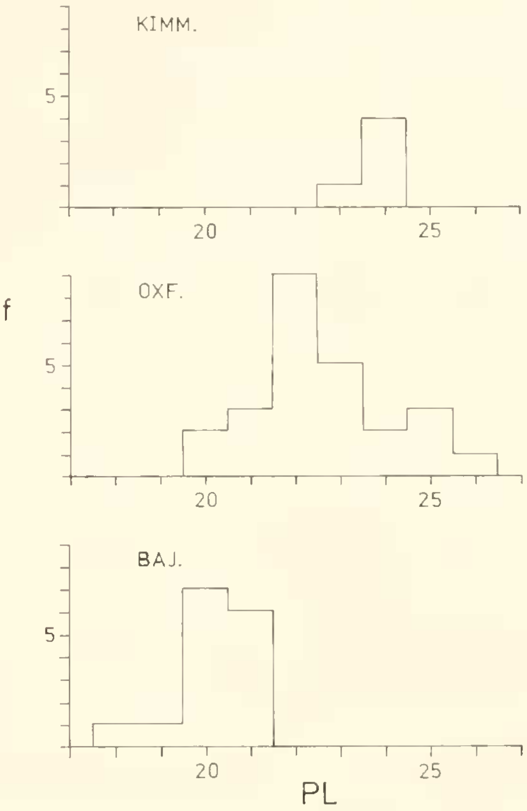
Text fig. 77: *Spondylopecten (S.) palinurus* – convexity/length.

Both valves bearing between 18 (? 16, see Section 4) and 26 rounded radial plicae; modal number apparently increasing phyletically (text fig. 79); plicae slightly wider than sulci in right valve, converse in left valve. Plicae bearing 4 rows of short, closely spaced spines, directed ventrally (Pl. 3, Fig. 14).

Cardinal area of right valve bearing 2 peg-shaped crura, anterior larger than posterior (Roeder, 1882, pl. 2, fig. 4). Shell thickness moderate to high; plical amplitude reduced on shell interior.



Text fig. 78: *Spondylopecten (S.) palinurus* – length/umbonal angle.



Text fig. 79: *Spondylopecten (S.) palinurus* – frequency distributions for number of plicae in Bajocian, Oxfordian and Kimmeridgian specimens.

4. DISCUSSION

d'Orbigny's (1850) diagnosis for '*Pecten*' *palinurus* (see Section 1) leaves no possibility of confusion for another Jurassic pectinid. Therefore, following Opinion 126 of the ICZN the name may be adopted for the species under discussion. Boule (1925) has figured one of the syntypes (MNO 3401) and this specimen is herein designated as lectotype. The other (also MNO 3401) becomes ipso facto the paralectotype. '*P.*' *Nireus* d'Orbigny was separated from '*P.*' *palinurus* on the basis of 'côtes plus simples', presumably implying a lack of spinose ornament. One of the syntypes (MNO 4294) possesses only two rows of spines per plica but this is clearly the result of abrasion (as appears to be the case in all the following instances where a reduced number of spine rows is cited) and H/L (1) and the number of plicae (23) are within the range of *S. (S.) palinurus* from the same stage (Oxfordian). '*P.*' *Nicaeus* d'Orbigny was separated on the basis of abnormally wide sulci. However, this feature is merely the result of preservation of the 6 syntypes (MNO 4295) as internal moulds (Boule, 1929) which has led to a reduction in plical amplitude and an apparent increase in plical wavelength.

The single known type of '*P.*' *symmetricus* Morris (IGS 8853; Pl. 3, Fig. 9) from the Bajocian has 20 plicae (2 spine rows) and is a typical example of *S. (S.) palinurus* from the stage.

'*P.*' *erinaceus* Buvignier (3 spine rows, 22–24 plicae) and '*P.*' ('*Chlamys*') *Roederi* de Loriol (24 plicae), both described from the Oxfordian, have plical counts and metric proportions of their respective figures (2, 3) which are inseparable from those of *S. (S.) palinurus* from the same stage. '*P.*' *araricus* Étallon was said to lack the spinose ornament of '*P.*' *erinaceus* but the figured specimen has clearly been subject to abrasion.

The holotypes (OD) of '*Ch.*' ('*Aequipecten*') *macfadyeni* Cox (BM L61138; Pl. 3, Fig. 11) from the Oxfordian/Kimmeridgian of E. Africa and '*Ch.*' *(S.) stoliczkai* Cox (IGS 17281) and '*Ch.*' *(S?) badiensis* Cox (BM L75245; Pl. 3, Fig. 12) from the Callovian of Cutch, all have their respective numbers of plicae (19, 20/21, 21/22) and metric proportions (4, 5, 6) within the total (stratigraphically undifferentiated) range of *S. (S.) palinurus*. The first and last appear to lack spines but may be abraded. Specimens from the Callovian of E. Africa referred to '*Ch.*' *(S.) badiensis* by Cox (1965) exhibit the characteristic spines. The holotype of '*Ch.*' ('*Ae.*') *macfadyeni* also has an abnormally small number of plicae for its particular stratigraphic horizon but this might well be an artefact of the relatively limited number of specimens for comparison,as is almost certainly the case for '*P.*' sp. Krumbeck, '*P.*' *Cartieri* de Loriol and '*P.*' *Monsbeliardensis* Contejean, all of which are from the Kimmeridgian and refer to specimens with respectively 22, and as many as 25 and 26 plicae. Krumbeck's specimens were compared with '*P.*' *erinaceus* Buvignier, a synonym of *S. (S.) palinurus* (see above),while metric proportions of the figures of de Loriol's (7) and Contjean's (8) specimens are indistinguishable from *S. (S.) palinurus*. The inclusion of '*P.*' *Soyhierensis* de Loriol (Oxfordian) within *S. (S.) palinurus* is more problematical since forms with as few as 16 plicae are cited and L/UA (9) of the original figure is somewhat low. However, '*P.*' *semiarticulatus* Meneghini (Bathonian), a species with 17 plicae and high L/UA (10), has the plical spine rows (albeit only 2 – see above) diagnostic of *S. (Spondylopecten)* and Dal Piaz (1912) has collected a topotype specimen, the figure of which has metric proportions (11) which are indistinguishable from *S. (S.) palinurus*. It therefore seems likely that the range of variation in the latter species extends considerably further than that indicated by museum specimens alone. '*P.*' *catulloi* Gemmellaro and Di Blasi (Tithonian), a species with 22 plicae known from only 4 specimens, may therefore by synonymous with *S. (S.) palinurus* in spite of the considerably atypical H/L, L/C and L/UA (12) of its original figure.

'*Ch.*' ('*Ae.*') *syriacus* Cossmann was said to have 30 plicae but the figures of the holotype (OD) reveal a maximum of only 21 and metric proportions (13) are within the total range of *S. (S.) palinurus*. With the possibility of misapplication of Cossmann's specific name to forms which are referable to *S. (S.) subpunctatus*, unfigured records of his species in R. Hudson (1958) must be treated with some caution.

The figures of '*P.*' *subpunctatus* Münster in Quenstedt (1858) and Remes (1903) and the descriptions in de Loriol (1904) and Simionescu (1910) are of specimens with respectively 25, 18–19, 24 and 22–26 plicae. All are thus outside the range of variation accredited to Münster's species (see p. 98) and fall within the total range of *S. (S.) palinurus*. The specimens referred to in Quenstedt and de Loriol are also within the range of variation in museum specimens of *S. (S.) palinurus* from the same stage (Oxfordian). There are insufficient museum specimens of comparable age (U. Tithonian) to allow an assessment of whether the same could be said of Remes' specimens. Those referred to in Simionescu are of indeterminate age.

'*P.*' *(S.) erinaceus* Buvignier; Yin (Tithonian) was not figured and was only distinguished from '*P.*' *(S.) globosus* Quenstedt; Yin (= *S. (S.) subpunctatus*) by its possession of less than 30 plicae. Since this does not exclude all variants of *S. (S.) subpunctatus* Yin's record is of uncertain status.

Although the exact dimensions of '*Ch.*' *Grossouvrei* Cossmann (Callovian) are not available the strongly convex form with 25 plicae is unlike that of any known Jurassic pectinid other than *S. (S.) palinurus*. For this reason '*Ae.*' *kotsubu* Kimura; Tamura, an inflated form with 22 plicae from the U. Jurassic of Japan may also be synonymous with *S. (S.) palinurus*. It has not been possible to trace Kimura's original description.

5. STRATIGRAPHIC RANGE

A poorly preserved specimen with 23 plicae (BM 30496) from the Spinatum zone (U. Pliensbachian) of Northants. might be an early representative of *S. (S.) palinurus*. However, apart from this there are no records of the species until the Garantiana and Parkinsoni zones (U. Bajocian) when, in the Cotswolds, the species is fairly common. Elsewhere *S. (S.) palinurus* is extremely rare in the U. Bajocian. Bathonian records are limited to N. Italy (G. Meneghini, 1880; Dal Piaz, 1912), and Indre (Cossmann, 1907a; J.-C. Fischer, 1964) and Var (BM L10289) in France although numerous specimens are recorded in all but the last area. In the Callovian the species is only known from occasional specimens from the Côte d'Or and Sarthe in France (d'Orbigny, 1850; Cossmann, 1912) and Cutch in India (Cox, 1952), and from E. Africa (Cox, 1965), Sinai (Douvillé and Cossmann, 1925), S. Israel (R. Hudson, 1958) and Arabia (BM L61511). In Europe *S. (S.) palinurus* reaches its acme in the Oxfordian and Kimmeridgian when it is locally abundant. Certain records from the Tithonian are restricted to one specimen from the lower substage at Nattheim (BM 63059). However, specimens described from the L. Tithonian of Sicily (Gemmellaro and Di Blasi, 1874; Gemmellaro, 1875) and the U. Tithonian of S. France (Yin, 1931) and Czechoslovakia (Remes, 1903) may well constitute further records of *S. (S.) palinurus* (see Section 4).

Text fig. 80: *Spondylopecten (S.) palinurus* – European distribution.

6. GEOGRAPHIC RANGE

In Europe (text fig. 80) the distribution of *S. (S.) palinurus* is intimately linked with that of coralliferous deposits (see Section 7). Thus the species occurs most commonly in the Oxfordian and Kimmeridgian of central W. Europe where this facies is particularly well developed. The lack of *S. (S.) palinurus* from coralliferous deposits in the Bathonian and Oxfordian of England and the Bathonian of Normandy suggests that the northward range of the species was restricted by temperature (however, see Section 8).

In the Callovian the range of *S. (S.) palinurus* underwent an expansion along the southern shores of Tethys, resulting in a palaeolatitudinal spread of some 50° (text fig. 81). A similar expansion along the northern shores is evidenced only by one dubious specimen from the U. Jurassic of Japan (see Section 4).

Text fig. 81: *Spondylopecten (S.) palinurus* – World distribution (Callovian reconstruction).

7. DESCRIPTION OF ECOLOGY

Bivalved specimens of *S. (S.) palinurus* are quite common in the Upper Coral Bed and its lateral equivalents in the Parkinsoni zone (U. Bajocian) of the southern Cotswolds. The maximum height attained is 26.5 mm (BM L84516). The associated fauna is dominated by the 'coarse' phenotype of *Ch. (Ch.) textoria*, *Limatula*, *Plagiostoma*, *Ctenostreon* and *Trigonia* together with the brachiopods *Rhynchonella*, *Terebratula* and *Zeilleria*, and the coral *Isastrea* (Richardson, 1907, 1910). *S. (S.) palinurus* also occurs in apparently non-coralliferous deposits of the Garantiana zone in the same area. However, the number of examples is small and only one specimen is known from non-coralliferous U. Bajocian deposits elsewhere in England. The modal number of plicae in specimens from the substage is 20, with a range from 18–21 (text fig. 79).

In the Bathonian *S. (S.) palinurus* occurs fairly commonly in N. Italy, where it reaches a maximum height of 25 mm (G. Meneghini, 1880; Dal Piaz, 1912) and in a coral bed in Indre (France) where it is associated with the 'coarse' phenotype of *Ch. (Ch.) textoria* (Cossmann, 1907a; J.-C. Fischer, 1964). The range of plical variation in Bathonian *S. (S.) palinurus* is from 17 (G. Meneghini, 1880) to 25 (Cossmann, 1907a).

Although widespread in the Callovian (see Sections 5, 6) *S. (S.) palinurus* is not known to be common anywhere. The range of plical variation in specimens from the stage is from 20 (e. g. Cossmann, 1912) to 23 (Cox, 1965) and the maximum height is 37 mm (MNS).

In the Oxfordian *S. (S.) palinurus* is very common in the coral/*Diceras* reefs of the Yonne, Meuse and Swiss and French Jura. In the last area it reaches a maximum height of 62 mm (de Loriol, 1894). The typical associated fauna is described on p. 88. The range of plical variation undoubtedly extends from 20–26 (mode 22) and may include forms with as few as 16 plicae (text-fig. 79; de Loriol, 1900).

In coral/*Diceras* facies in the Kimmeridgian of the Jura *S. (S.) palinurus* is common and appears to reach a maximum height of 35 mm (Contejean, 1859). There is an abundant associated molluscan fauna of in- and epifaunal gastropods and bivalves (including the byssate genera *Camptonectes*, *Oxytoma*, *Pinna*, *Arca* and '*Mytilus*') together with rhynchonellid brachiopods. Only one specimen (GPIG) is known from contemporaneous coral patch reef facies at La Rochelle and none are recorded from similar facies at Kelheim (S. Germany). The range of plical variation in Kimmeridgian *S. (S.) palinurus* is from 22–26 (text fig. 79; Contejean, 1859; Krumbeck, 1905) with a mode of 24.

The single undoubted Tithonian example of *S. (S.) palinurus* together with other putative records from the stage (see Section 5) are all from coral reef facies (fauna p. 88).

There are no records of *S. (S.) palinurus* from the deep water pelagic limestones of the peri-Mediterranean region and the species is very rare in siliciclastic deposits anywhere in Europe.

8. INTERPRETATION OF ECOLOGY

The data presented in Section 7 suggest very strongly that the occurrence of *S. (S.) palinurus* is dependent on the presence of corals. Reefs appear to have constituted the most favourable habitat but the fact that the species occurs in coral accumulations of less than reefal dimensions (Parkinsoni zone, S. Cotswolds; Bathonian, Indre) suggests that the particular abundance in reefs is merely a reflection of the concentration of corals rather than a consequence of a preference for upstanding structures (cf. Hertlein, 1969; Hallam, 1976; see pp. 83, 88). The correspondence between the areal distribution of coralliferous deposits and that of common *S. (S.) palinurus* in the Parkinsoni zone of N. Somerset and Gloucestershire is striking enough to be an incentive for a facies analysis of the underlying Garantiana zone deposits in order to test the possibility that the examples of *S. (S.) palinurus* contained therein might be derived from laterally equivalent but unexposed coralliferous deposits. Similarly the fact that the only occurrence in the Bathonian and Callovian where facies are known (Bathonian, Indre) is from a coral bed containing the reef-dwelling 'coarse' phenotype of *Ch. (Ch.) textoria* should be an impetus for analyses of the sediments and fauna of the other horizons containing *S. (S.) palinurus* in these stages.

In spite of the apparent dependence on corals by no means all coralliferous horizons within the stratigraphic range of *S. (S.) palinurus* were colonised abundantly. The fact that during the Kimmeridgian coral patch reefs at the southerly latitudes of La Rochelle and Kelheim were only colonised very rarely or not at all, while during the Bajocian coralliferous deposits in England were occupied in numbers, suggests that the complete absence of *S. (S.) palinurus* from Bathonian coral patch reefs in Normandy and England and similar facies in the Oxfordian of England cannot be the result of a simple temperature dependence (see p. 95) or even of a more general intolerance of relatively unstable environments (see p. 89). In certain of the above cases the lack of *S. (S.) palinurus* could be a consequence of the particular coral fauna of the reefs and their resultant dense structure, an explanation advanced for the absence or rarity of *S. (Pl.) subspinosus* (see p. 88). However, the Oxfordian reefs of England do not seem to have had an especially dense structure (see p. 89). Evidence from the L. Tithonian reef at Nattheim, where *S. (S.) palinurus* is extremely rare but *S. (Pl.) subspinosus* is abundant, suggests a more specific control on distribution. For an alternative explanation one might invoke the possibility (see p. 89) of a commensal relationship between particular coral species and each of *S. (Pl.) subspinosus* and *S. (S.) palinurus*, and infer the absence of the relevant corals from the reefs lacking these *Spondylopecten* species. However, such an explanation suffers generally from the lack of any direct evidence for commensalism and specifically, in the case of *S. (S.) palinurus*, from the fact that in the Nattheim reef the latter species is very rare although coral diversity is high, 64 species being cited by Geyer (1954). It must therefore be admitted that no unified theory can yet be proposed to account for the inconsistent distribution of *S. (Pl.) subspinosus* and *S. (S.) palinurus* in coralliferous facies (see p. 101).

The overall rarity of *S. (S.) palinurus* in the M. Jurassic of Europe as a whole can be viewed as a consequence of the localised development of coralliferous deposits. The very widespread development of argillaceous facies in the Callovian, producing unfavourable conditions for coral growth, may well have prompted the migration of *S. (S.) palinurus* outside Europe along the southern shores of Tethys (see Section 6).

The usual occurrence of *S. (S.) palinurus* in moderate numbers with a high diversity fauna indicates that it was an equilibrium species (Levinton, 1970). Presumably stenotopy was developed to a high enough degree to prevent competition with the other species of *Spondylopecten* with which it frequently occurs.

9. FUNCTIONAL MORPHOLOGY

In the absence of more precise ecological data for *S. (S.) palinurus* little can be added to the general interpretation of functional morphology in *Spondylopecten* presented for the essentially similar species *S. (Pl.) subspinosus* (see p. 89). A 'wedged' mode of life is further evidenced by the great variation in convexity in *S. (S.) palinurus*. However, as for *S. (Pl.) subspinosus* it cannot yet be said definitely that this is a positively adaptive feature brought about by developmental flexibility (however, see below).

The moderately large maximum height of *S. (S.) palinurus* (H: 62) is near the upper limit for byssally attached Recent pectinids. The largest byssate but otherwise unsupported species from the coral reef fauna of Eniwetok Atoll *(Gloripallium pallium)* reaches a maximum height of 85 mm. However, this and other pendent or tightly byssate species rarely exceed a height of 75 mm (Waller, 1972b). It therefore seems likely that large specimens of *S. (S.) palinurus* gained support, additional to that provided by the byssus, through contact with the substrate, as inferred independently above.

The moderate to high convexity and shell thickness in *S. (S.) palinurus* suggest that at best it could only have been a very inefficient swimmer.

The apparent phyletic increase in the number of plicae may be interpreted mechanically when considered in conjunction with phyletic decrease in convexity and increase in height (see Section 10). The latter requires relatively large amounts of $CaCO_3$ to be secreted when growth is based on a tight logarithmic spiral as in *S. (S.) palinurus*. A decrease in the spiral angle and hence in convexity thus represents a more bioeconomical basis for height increase. However, it must also entail a weakening of the shell so an increase in the number of plicae can be viewed as an attempt to strengthen and stiffen the shell by effectively shortening the wavelength of the corrugations. Such an interpretation requires however that the increased strength and stiffness contribute significantly to the fitness of the animal as a whole. This must be considered doubtful in *S. (S.) palinurus* since the thickness of the shell would appear to provide adequate protection against all but the most extreme stresses. Nevertheless, the impression gained by the author that the variation in convexity and number of plicae is positively correlated at any one horizon indicates that there is at least some functional interdependence and suggests moreover that *S. (S.) palinurus* is developmentally flexible (see above).

10. ORIGINS AND EVOLUTION

If the very doubtful record of *S. (S.) palinurus* in the U. Pliensbachian is discounted, *S. (S.) subpunctatus* becomes the most likely ancestor for the species (although see p. 101). There is no evidence to suggest that the evolution of a separate pattern of plical variation occurred gradually.

There appear to be several phyletic trends within *S. (S.) palinurus*. Maximum height increases, presumably gradually, from 26.5 mm (U. Bajocian) to 37 mm (Callovian) to 62 mm (Oxfordian). The reversal of this trend in the Kimmeridgian (H_{max}: 35) could well be an artefact of the relatively limited number of specimens from the stage measured by the author. The pronounced phyletic increase in the mean number of plicae indicated by text fig. 79 might also be an artefact of the more general paucity of measured museum specimens since bibliographic sources (see Section 4) suggest a far less consistent trend. Nevertheless, specimens mentioned in the literature do not refute the gradual unidirectional trend in the modal number of plicae indicated by text fig. 79. Indeed the 15 or so specimens collected by Cox (1952) from the Callovian of Cutch which were said to have a range of between 20 and 22 plicae (exactly between the Bajocian and Oxfordian modes) provide positive evidence for such a trend. Only one of the other Callovian records (Cox, 1965 for two specimens with 23 plicae) refers to specimens with plical counts outside the latter range.

A further phyletic trend is towards decreased convexity. However, unlike the above cases there is little reason to think that evolution occurred gradually. Most Callovian, Oxfordian and Kimmeridgian specimens have lower C/L ratios than their Bajocian ancestors (text fig. 77). Since relative convexity appears to increase during the ontogeny of the latter there is the possibility that descendant forms could have arisen by neoteny. However, heterochrony cannot account for the periodic phyletic increases in the ranges of plical variation constituted by specimens mentioned in the literature together with those in museums (Bajocian, 18–21; Bathonian, 17–25; Callovian, 20–23; Oxfordian, 20–26; Kimmeridgian, 22–26) thus phyletic evolution in *S. (S.) palinurus* may generally have been a product of change in the structural rather than the regulatory genome.

Phyletic increase in maximum height combined with stenotopy and a possibility of neoteny suggests the prevalence of 'K' selection for increased trophic efficiency (Gould, 1977).

Spondylopecten (Spondylopecten) subpunctatus (Münster 1833)

Pl. 3, Figs. 15–19; text figs. 75 (pars), 82–86

Synonymy

v* 1833	*Pecten subpunctatus* sp. nov; Münster in Goldfuss, p. 48, pl. 90, figs. 13a, 13b.
1843	*Pecten subpunctatus* Münster; Quenstedt, p. 433.
p 1843	*Pecten globosus* sp. nov; Quenstedt, p. 476.
1850	*Pecten subpunctatus* Münster;d'Orbigny, v. 1, p.374.
1852	*Pecten Moreanus* sp. nov; Buvignier, p. 24, pl. 19, figs. 18–20.
1852	*Pecten globosus* Quenstedt; Quenstedt, p. 507, pl. 40, fig. 45, (non fig. 46; non Quenstedt sp.).
non 1858	*Pecten subpunctatus* Münster; Quenstedt, p. 627, pl. 77, figs. 27–29.
v* 1858	*Pecten aequatus* sp. nov; Quenstedt, p. 755, pl. 92, fig. 12.
1858	*Pecten globosus* Quenstedt; Quenstedt, pl. 78, fig. 2 (non pl. 92, fig. 20; non Quenstedt sp.).
1862	*Pecten Globosus* Quenstedt; Thurmann and Êtallon, p. 250.
1866	*Pecten subpunctatus* Münster; Oppel, p. 289.
1867	*Pecten globosus* Quenstedt; de Loriol, p. 335, pl. 13, fig. 3 (non Quenstedt sp.).
1867	*Pecten Rochati* sp. nov; de Loriol, p. 336, pl. 13, figs. 1, 2.
1874	*Pecten arotoplicus* sp. nov; Gemmellaro and Di Blasi, p. 104, pl. 2, figs. 6–10.
1875	*Pecten arotoplicus* Gemmellaro and Di Blasi; Gemmellaro, p. 41.
1881a	*Pecten aequatus* Quenstedt; Boehm, p. 183.
1881b	*Pecten aequatus* Quenstedt; Boehm, p. 72.
v 1883	*Pecten arotoplicus* Gemmellaro and Di Blasi; Boehm, p. 609, pl. 67, figs. 34, 35.

? 1886a	*Pecten erpus* sp. nov; De Gregorio, p. 670, pl. 1, fig. 8.
? 1893	*Pecten globosa* Quenstedt; Siemiradzki, p. 119.
1894	*Pecten Moreanus* Buvignier; de Loriol, p. 40, pl. 4, fig. 12.
1898	*Pecten globosus* Quenstedt; E. Philippi, p. 620, text figs. 6, 7 (non Quenstedt sp.).
? 1898	*Pecten (Chlamys) erpus* De Gregorio; Greco, p. 110, pl. 8, figs. 32, 33.
1903	*Pecten arotoplicatus* Gemmellaro and Di Blasi; Remes, p. 202.
1903	*Pecten Rochati* de Loriol; Remes, p. 202, pl. 19, figs. 5a–c.
1903	*Pecten Gemmellaroi* sp. nov; Remes, p. 202, pl. 19, figs. 7a–c.
non 1903	*Pecten subpunctatus* Münster; Remes, p. 203, pl. 19, figs. 8a–c.
1903	*Pecten (Spondylopecten) globosus* Quenstedt; Remes, p. 205 (non Quenstedt sp.).
non 1904	*Pecten subpunctatus* Münster; de Loriol, p. 217, pl. 23, fig. 4.
v 1905	*Pecten moreanus* Buvignier; Peron, p. 213.
1905	*Pecten palmyrensis* sp. nov; Krumbeck, p. 102, pl. 3, figs. 8a, 8b.
? *1905*	*Pecten (Chlamys) globosus* Quenstedt; Kilian and Guébhard, p. 817.
non 1910	*Pecten subpunctatus* Münster; Simionescu, p. 14.
1910	*Pecten moreanus* Buvignier: Simionescu, p. 14, pl. 2, fig. 6.
1913	*Pecten globosus* Quenstedt; Joukowsky and Favre, p. 400, pl. 17, figs. 3–6 (non Quenstedt sp.).
1920	*Pecten aratoplicus* Gemmellaro and Di Blasi; Faure-Marguerit, p. 58.
1920	*Pecten (Spondylopecten) globosus* Quenstedt; Faure-Marguerit, p. 60, (non Quenstedt sp.).
v 1926	*Spondylopecten subpunctatus* (Münster); Staesche, p. 109, pl. 4, fig. 10.
1926	*Spondylopecten aequatus* (Quenstedt); Staesche, p. 112.
1931	*Pecten (Spondylopecten) globosus* Quenstedt; Yin, p. 118, pl. 12, figs. 3–6 (non Quenstedt sp.).
? 1931	*Pecten (Spondylopecten) erinaceus* Buvignier; Yin, p. 119 (non Buvignier sp.).
? 1931	*Pecten* aff. *subpunctatus* Münster; Yin, p. 122.
1936	*Spondylopecten moreanus* (Buvignier); Dechaseaux, p. 67.
? *1959*	*Spondylopecten globosus* (Quenstedt); Hölder and Ziegler, p. 165.
1966	*Spondylopecten aequatus* (Quenstedt); Karve-Corvinus, p. 115.
(?) *1971*	*Chlamys* cf. *erpus* (De Gregorio); Wendt, p. 156.
v 1975	*Spondylopecten aequatus* (Quenstedt); Yamani, p. 64, pl. 3, fig. 10.
v* 1975	*Spondylopecten proumbonatus* sp. nov; Yamani, p. 64, pl. 3, figs. 11, 12.

Lectotype of *Pecten subpunctatus* Münster in Goldfuss 1833, p. 48, pl. 90, fig. 13 designated herein; BSPHG AS VII 627; Pl. 3, Fig. 15 herein; Weisser Jura β (Oxfordian), Streitberg (Franconia). Paralectotypes; the 9 other syntypes (BSPHG); also Weisser Jura β, Streitberg.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

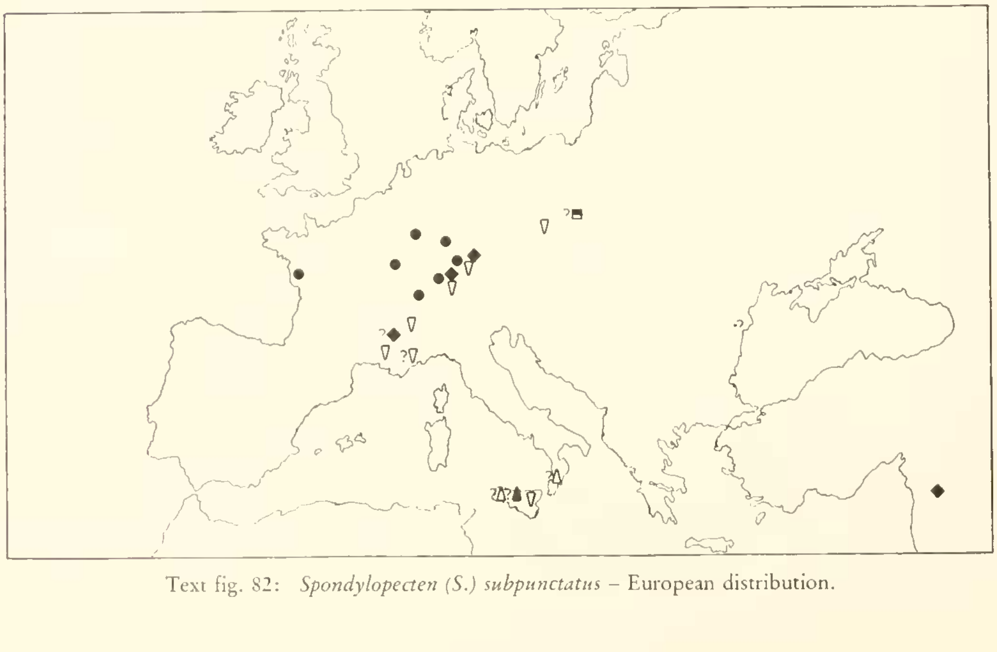
'Pecten testa suborbiculari fornicata, costis crebris convexis marginalibus muricatus, sulcis angusti, oribus in fundo plano profunde transversim striatis, auriculis aequalibus.

E montibus Baruthinis M. M.

Dieser kleine Pectinit findet sich bei Streitberg. Er ist hoch gewölbt, gleichklappig, fast kreisrund, und hat zahlreiche, convexe, gleichförmige Rippen, auf deren Rücken man bei der Vergrößerung stachelförmige Lamellen bemerkt. Die Zwischenfurchen sind concentrisch liniert, so daß sie ein punktiertes Ansehen haben, und die Ohren klein und gleichförmig.'

2. AMENDED DIAGNOSIS

Distinguished from all other species of *S. (Spondylopecten)* by the number of plicae (27–36 or 37, see Section 4).

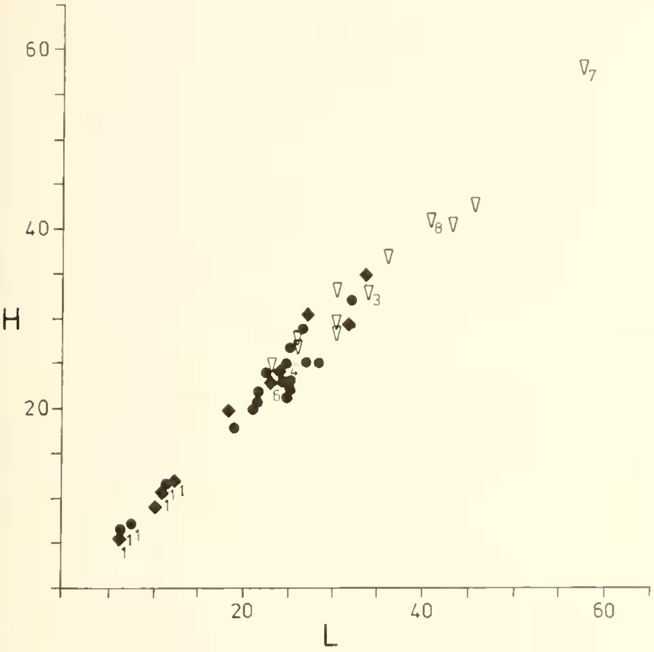


Text fig. 82: *Spondylopecten (S.) subpunctatus* – European distribution.

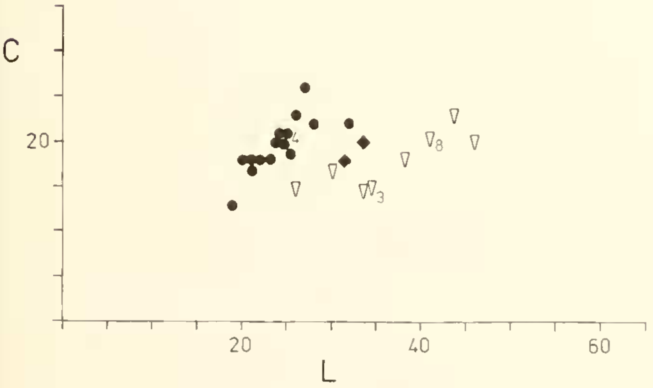
3. AMENDED DESCRIPTION

Essentially similar to *S. (S.) palinurus*. Differing by the diagnostic larger number of plicae (see Section 2) whose range and mode apparently oscillates phyletically (text fig. 86), by the evident possession of only 2 plical spine rows, and by the higher relative convexity (text fig. 84) of contemporaneous Oxfordian specimens and the lower relative convexity of Tithonian forms of *S. (S.) subpunctatus* in comparison with examples of *S. (S.) palinurus* from any horizon. Unlike *S. (S.) palinurus*, *S. (S.) subpunctatus* also exhibits phyletic reduction in L/UA (text fig. 85) although this could be more apparent than real (see Section 9).

H/L is plotted in text fig. 83. The maximum height is 58 mm (Gemmellaro and Di Blasi, 1874).



Text fig. 83: *Spondylopecten (S.) subpunctatus* – height/length.



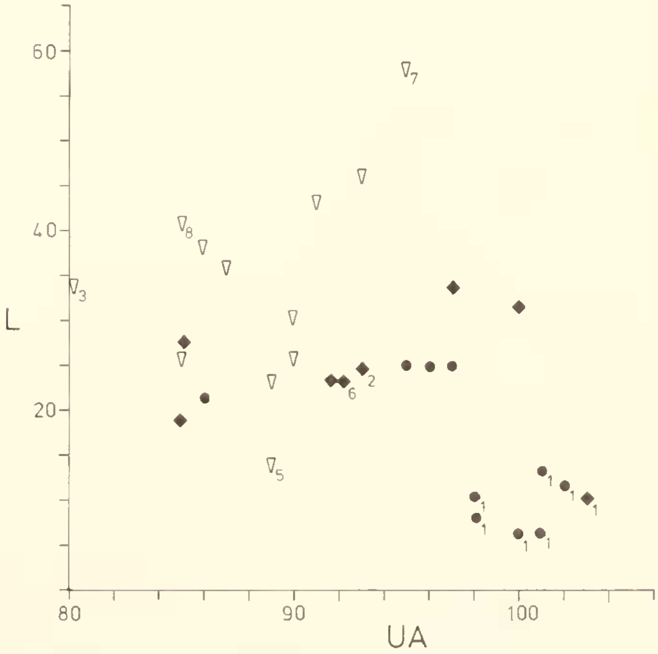
Text fig. 84: *Spondylopecten (S.) subpunctatus* – convexity/length.

4. DISCUSSION

The syntype series of *'P.' subpunctatus* Münster (BSPHG) consists of a number of specimens from sponge-limestone facies, all less than 10 mm in height and with approximately 30 plicae. Staesche (1926) considered such specimens to be specifically separable from juveniles of a similarly plicate form, *Spondylopecten aequatus* (Quenstedt), from coral reef facies, on the basis of the flat tops to the plicae. However, this feature together with a relatively large umbonal angle (1) can be plausibly interpreted as an aspect of ecophenotypic variation (see Section 8) and is therefore no basis for a specific distinction. Thus, on grounds of historical precedence Münster's specific name is applied to the species described in Section 3 and a lectotype (BSPHG AS VII 627; Pl. 3, Fig. 15) is herein designated. Those specimens incorrectly referred to Münster's species in Quenstedt (1858), Remes (1903), de Loriol (1904) and Simionescu (1910) are discussed on p. 94. The two specimens said by Yin (1931) to have affinities with Münster's species are of uncertain status since they were not illustrated and were described only as having numerous ribs. Specimens referred by Yin to *'P.' (Spondylopecten) erinaceus* Buvignier were described with similar imprecision and may be referable to either *S. (S.) subpunctatus* or *S. (S.) palinurus* (q. v.).

Quenstedt's specific name *'P.' globosus* has been variously employed in the literature (discussion p. 104) on account of the vagueness of the original description (1843) and the fact that the name was subsequently applied by Quenstedt (1852, 1858) to illustrations of both a specimen with about 60 plicae and a specimen with about 30 plicae. The latter is indistinguishable from *S. (S.) subpunctatus*, as are specimens from the Oxfordian with 32 plicae referred to Quenstedt's species by Thurmann and Étallon (1862) and specimens from the Tithonian with 32, 30, 30, 32, 30–35 and 34 plicae referred to Quenstedt's species by, respectively, de Loriol (1867), Philippi (1898), Remes (1903), Joukowsky and Favre (1913), Faure-Marguerit (1920) and Yin (1931). Specimens referred to Quenstedt's species by Siemiradzki (1893), Kilian and Guebhard (1905) and Hölder and Ziegler (1959) are of uncertain status because the number of plicae was not stated.

The sole observed type (GPIT 4-92-12; Pl. 3, Fig. 17) of *'P.' aequatus* Quenstedt (Kimmeridgian) and the holotype



Text fig. 85: *Spondylopecten (S.) subpunctatus* – length/umbonal angle.

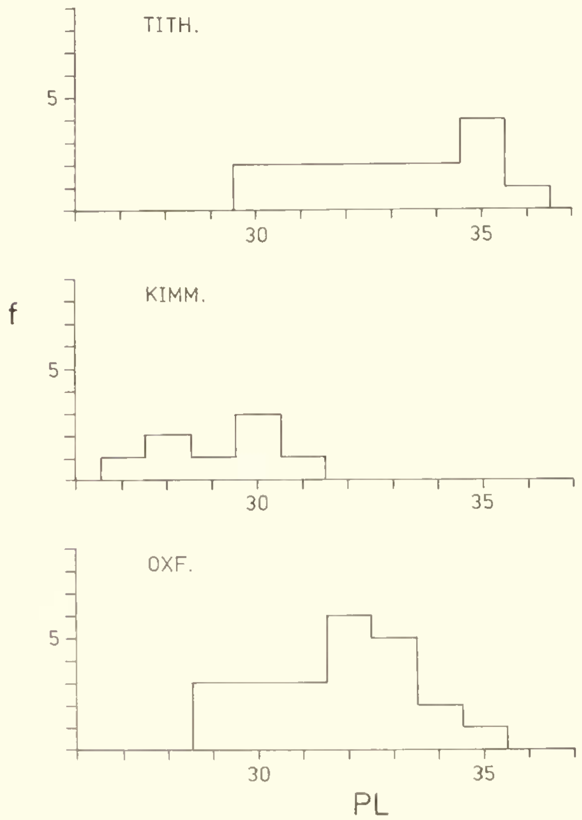
(OD; BSPHG 1957 II 329; Pl. 3, Fig. 18) of *S. proumbonatus* Yamani (Tithonian) have respective numbers of plicae (28, 31) and metric proportions (2, 3) that are indistinguishable from those of *S. (S.) subpunctatus* from comparable horizons. Similarly the plical counts and metric proportions (32–34; 4) supplied by Buvignier (1852) for '*P.*' *Moreanus* (Oxfordian) and derived from the figures of '*P.*' *Gemmellaroi* Remes (Tithonian; 35; 5) and '*P.*' *Palmyrensis* Krumbeck (Kimmeridgian; 28; 6) are inseparable from those of *S. (S.) subpunctatus* from the appropriate horizon.

'*P.*' *arotoplicus* Gemmellaro and Di Blasi (Tithonian) has a plical count (32) within the range of *S. (S.) subpunctatus* from the same stage and the large umbonal angle (95°) cited by the authors appears to be nothing more than a consequence of large size since L/UA (7) is within the range of projected Tithonian ontogenies. '*P.*' *Rochati* de Loriol, also from the Tithonian, has metric proportions (8) of the single known specimen which are indistinguishable from those of *S. (S.) subpunctatus* from the same stage. It therefore seems extremely likely that the abnormally large number of plicae (37) represents extreme variation within *S. (S.) subpunctatus*.

'*P.*' *erpus* De Gregorio was erected for a specimen from the Aalenian of Sicily whose number of plicae (28) and high convexity suggest strongly that it is conspecific with *S. (S.) subpunctatus*. Greco (1898) has figured a further specimen with 32 plicae from the Aalenian of Calabria under the same specific name.

5. STRATIGRAPHIC RANGE

Assuming that '*P.*' *erpus* is synonymous with *S. (S.) subpunctatus* (see Section 4) the earliest records of the latter species are from the Opalinum zone of Calabria (Greco, 1898) and the Murchisonae zone of Sicily (De Gregorio, 1886a). Wendt (1971) considers that De Gregorio's species ranges into the U. Bajocian in the latter area. Otherwise *S. (S.) subpunctatus* is unknown before the Oxfordian, when it is locally abundant. It is found thus until the U. Tithonian (Boehm, 1883; Remes, 1903; Faure-Marguerit, 1920; Yin, 1931). The lack of Bathonian and Callovian records and the consequent doubt that this attaches to the systematic position of '*P.*' *erpus* could well be due to the rarity of the favoured reefal facies in Europe (see Sections 7, 8).



Text fig. 86: *Spondylopecten (S.) subpunctatus* – frequency distributions for number of plicae in Oxfordian, Kimmeridgian and Tithonian specimens.

6. GEOGRAPHIC RANGE

The distribution of *S. (S.) subpunctatus* within Europe (text fig. 82) is intimately linked with that of reefal deposits (see Sections 7, 8). Thus during its acme in the U. Jurassic the species occurs most abundantly in S. Europe where this facies is particularly well developed. The only record outside Europe is from Kimmeridgian coral-bearing limestones in the Lebanon (Krumbeck, 1905).

The absence of *S. (S.) subpunctatus* from reefal deposits in the Oxfordian of England may indicate that latitudinal temperature changes played some part in controlling the distribution of the species (however, see Section 8).

The absence of *S. (S.) subpunctatus* from L. Bajocian coral reefs in E. France need not affect the taxonomic status of roughly contemporaneous specimens referred to '*P.*' *erpus* from S. Italy and Sicily (see Sections 4, 5). The latter areas probably lay near the south side of Tethys thus it could be that *S. (S.) subpunctatus* arose in that region and had insufficient time to spread to more northerly latitudes before the L. Bajocian. In any case there are some grounds for thinking (see p. 89) that reefs with a structure such as that of the L. Bajocian reefs in E. France may have constituted an unfavourable environment for *Spondylopecten*.

7. DESCRIPTION OF ECOLOGY

The putative early records of *S. (S.) subpunctatus* from the Aalenian and Bajocian of Sicily (see Section 5) are from condensed deposits probably formed on a guyot within the Tethyan ocean. Occasional intercalations of coral debris suggest that reefs were periodically developed nearby (Wendt, 1963, 1971).

The species occurs abundantly in the Oxfordian coral reefs of the Yonne (Peron, 1905) and Swiss Jura (de Loriol, 1894) in association with the fauna described on p. 88. The maximum height of Oxfordian *S. (S.) subpunctatus* is 32 mm (MNS) and the range of plical variation (text fig. 86) is from 29–35 (mode: 32).

Sponge 'reef' facies in the Oxfordian and Kimmeridgian of S. Germany contain numerous *S. (S.) subpunctatus* but the adult height is rarely more than 5–7 mm (Staesche, 1926). The plicae are also flat-topped and the L/UA ratio (1) is typically low compared to specimens from coral reefs. Examples from the latter facies in the Kimmeridgian at Kelheim (S. Germany) reach a maximum height of 35 mm (GPIT) and are associated with a rich bivalve fauna (Boehm, 1881a, b) while those from sponge 'reef' facies are typically associated with a low diversity/density bivalve fauna in which *Isoarca* is the only form to occur in numbers (Nitzopoulos, 1974). *S. (S.) palinurus* seems to be absent from the Kelheim reef but it is common in coral/*Diceras* facies in the Kimmeridgian of the Jura where *S. (S.) subpunctatus* is unknown. The latter is also absent from contemporaneous coral reefs at La Rochelle but *S. (S.) palinurus* is in addition extremely rare.

The range of plical variation in Kimmeridgian *S. (S.) subpunctatus* is from 27–31 (text fig. 86) and forms from reefal facies seem to have a relatively high L/UA (text fig. 85) and C/L (text fig. 84) compared to their Oxfordian counterparts.

In the Tithonian *S. (S.) subpunctatus* occurs, often in abundance, in the coral reefs of Languedoc (Yin, 1931) and Isère (Faure-Marguerit, 1920) in S. France, Geneva in Switzerland (de Loriol, 1867) Arnegg, Neuberg, Nattheim, Sirchingen and Wittlingen in S. Germany (GPIT; Staesche, 1926; Yamani, 1975), Stramberg in Czechoslovakia (Boehm, 1883; Remes, 1903) and near Palermo in Sicily (Gemmellaro and di Blasi, 1874; Gemmellaro, 1875) where the species reaches a maximum height of 58 mm. The range of plical variation is from 30–37 with a mode of 35 (text fig. 86; de Loriol, 1867) and L/UA (text fig. 85) and C/L (text fig. 84) are large compared to Kimmeridgian and Oxfordian forms. The typical associated fauna is described on p. 88. *S. (S.) palinurus* is only known to be an associate at Nattheim and there very rarely. However, it may also be present in Sicily, Provence and Czechoslovakia (see p. 94).

Apart from the occurrences discussed above *S. (S.) subpunctatus* is a rare species and none of the other definite records (see Synonymy) are unrelated to the development of reefal facies.

8. INTERPRETATION OF ECOLOGY

S. (S.) subpunctatus is an exemplar of the standard view (Hertlein 1969; Hallam, 1976) that *Spondylopecten* is a reef-restricted genus. There is no evidence that anything other than reefs were colonised during the U. Jurassic acme of *S. (S.) subpunctatus* thus the absence of the species from such minor coral stands as were colonised by the less restricted *S. (S.) palinurus* in the M. Jurassic of Europe need not be construed as evidence against the view that *'P.' erpus* is synonymous with *S. (S.) subpunctatus* (see Section 4). The absence of *S. (S.) subpunctatus* from genuine coral reefs in the L. Bajocian of E. France can be explained plausibly in several ways (see Section 6) while the general absence of the species from other bioherms in the M. Jurassic of Europe (see Section 5) could be due to their small size and scattered distribution.

Although a temperature dependence might account for the absence of *S. (S.) subpunctatus* from some U. Jurassic reefs (see Section 6) the inconsistent distribution in reefs of the same palaeolatitude argues against the general applicability of such an explanation. The abundance of other *Spondylopecten* species in some of the reefs lacking *S. (S.) subpunctatus* rules out an appeal to the unsuitability of the general reef structure (see p. 88) while an explanation in terms of a specific commensal relationship (see p. 96) is excluded by the evidence that *S. (S.) subpunctatus* used both corals and sponges as host. The inverse correlation in numbers with *S. (S.) palinurus* at certain localities in the Kimmeridgian and Tithonian suggests a further possible explanation for the irregular distribution of *S. (S.) subpunctatus* in the form of competition. However, the co-occurrence of the two species in large numbers in the Oxfordian (and probably at some localities in the Tithonian) argues against this hypothesis. In any case, if *Spondylopecten* species occupied different microhabitats (see p. 89) it seems unlikely that they would have competed. .

The small size, low L/UA and flattened plicae of *S. (S.) subpunctatus* in sponge 'reef' compared to coral reef facies can be attributed to stunting (see p. 99). Retardation of the rate of size (L) increase while shape (UA) development maintained the same rate would result in small absolute size and low L/UA, and the small size for any given age would cause increased abrasion by the substrate of a standard area of shell surface and could thus be expected to lead to relatively flattened plicae. The small size of the associated faunal elements is further suggestive of the occurrence of stunting although an analysis of growth lines is required to substantiate the hypothesis. Since Nitzopoulos (1974) estimates the depth of the sponge 'reefs' to have been between 50 and 100 m (compared with a maximum of a few tens of metres for coral reefs) an attractive explanation for stunting is available in terms of the reduced food supply characteristic of greater depths (Fürsich and Hurst, 1974).

9. FUNCTIONAL MORPHOLOGY

As for *S. (S.) palinurus* little can be added to the general interpretation of functional morphology in *Spondylopecten* presented on p. 89. Variation in convexity provides support for the inference of a 'wedged' mode of life and the higher convexity of *S. (S.) subpunctatus* compared to *S. (S.) palinurus* in contemporary populations implies that the former species occupied crevices, fissures etc. of a larger size.

Phyletic decrease in relative convexity might be explained as a bioeconomical correlate of increased size, as has been suggested for *S. (S.) palinurus* (but see Section 10). However, unlike the latter species there is no compensatory directional change in the strength and stiffness provided by shell ornamentation, since the mode and range of plical variation seems to oscillate at random. It is the author's impression, nevertheless, that there is a positive correlation between convexity and number of plicae at any one horizon so at least some mechanical interdependence is implied, which may in turn be related to phyletic size change.

The apparent phyletic decrease in relative umbonal angle receives no obvious mechanical explanation and may simply be an artefact of the measuring technique superimposed on the 'proumbonate' form (Yamani, 1975) of later populations.

The maximum height of 58 mm is within the size range of 'unsupported' bysally attached Recent pectinids (see p. 97) thus *S. (S.) subpunctatus* was probably byssate throughout ontogeny. The inflated form suggests that if it did ever unattach itself *S. (S.) subpunctatus* could only have been a very poor swimmer.

10. ORIGINS AND EVOLUTION

If *S. (S.) subpunctatus* arose after the Bajocian it is most reasonable to conclude that *S. (S.) palinurus* was the ancestor rather than vice versa as suggested on p. 97). However, if, as seems very probable (see Section 5, 7, 8), *S. (S.) subpunctatus* arose in the Aalenian no ancestor is available within the same subgenus. There is no particular reason for concluding that *S. (Plesiopecten) subspinosus* must be the ancestor (see p. 83) and indeed on gross morphological grounds it would seem likely that *S. (S.) subpunctatus* arose from a quite separate stock. The first apparent occurrence of the species (Aalenian; S. Italy, Sicily), outside what subsequently became the main geographic range, provides evidence for such a view and also supports the 'allopatric' model of speciation.

S. (S.) subpunctatus exhibits some evidence for gradual phyletic evolution. Maximum height increases from 32 mm (Oxfordian) to 35 mm (Kimmeridgian) to 58 mm (Tithonian) and within the limits of the available data there appears to be a similar increase through this interval in L/C and L/UA (although see Section 9) of specimens from coral reef facies. Since both L/C and L/UA seem to increase allometrically in ancestral (Oxfordian) populations descendant forms may have arisen by the acceleration of shape development with respect to size. However, heterochrony cannot account for the periodic phyletic additions to the range of plical variation (Oxfordian 29–35, Kimmeridgian 27–31, Tithonian 30–36) so both structural and regulatory genome evolution is implied.

Size increase and stenotopy are suggestive of 'K' selection in the evolution of *S. (S.) subpunctatus*. The possible occurrence of acceleration is however more suggestive of 'r' selection (Gould, 1977).

Phyletic reduction in relative convexity at least after the Kimmeridgian might have been allowed by the vacation of the appropriate niche through the decline of the relatively low convexity species *S. (S.) palinurus*. The mean C/L of Tithonian *S. (S.) subpunctatus* is however considerably lower than that of *S. (S.) palinurus* at any time and besides the decline in *S. (S.) palinurus* may be more apparent than real (see p. 94). An alternative explanation for the reduction in convexity is suggested in Section 9.

Spondylopecten (Spondylopecten) cardinatus
(Quenstedt 1858)

Pl. 3, Figs. 20, 21; text fig. 87

Synonymy

1858 *Pecten cardinatus* sp. nov; Quenstedt, p. 627, pl. 78, fig. 1.
v 1883 *Pecten spinicostatus* sp. nov; Whidborne, p. 502, pl. 15, figs. 14, 14a.
1916 *Aequipecten spinicostatus* (Whidborne); Paris and Richardson, p. 522.
1926 *Spondylopecten cardinatus* (Quenstedt); Staesche, p. 110.
p 1931 *Pecten cordiformis* Gemmellaro and Di Blasi; Yin, p. 119, pl. 12, fig. 7, pl. 13, fig. 7 (non Gemmellaro and Di Blasi sp.).

No trace of the type material of *Pecten cardinatus* Quenstedt 1858, p. 627, pl. 78, fig. 1 has yet been found in the Quenstedt Collection (GPIT). The figured specimen was derived from the Weisser Jura γ (Kimmeridgian) of Heuburg, S. Germany.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

‚Werden die Formen größer, dann treten zwar Unsicherheiten in der Bestimmung ein, doch will ich noch einen davon als *Pecten cardinatus* Tab. 78, Fig. 1 unterscheiden. Die Form nach schließt er sich an *globosus* Fig. 2 an, aber feine Rippen sind viel breiter. Ich würde ihn dennoch *globosus* γ genannt haben, wenn nicht der Name 'eingezapft' passend auf die Schloßzähne anspielte, welche ich bereits in Handb. Petref. Pag. 507 nachwies. Diese Zahnung des Schlosses ist bei verkieselten so eigentümlich, daß vielleicht später daraus eine besondere Gruppe Cardinaten gemacht werden kann. Kann ich auch bei diesen Verkalkten die Zähne nicht nachweisen, so ist wegen der Analogie an der Existenz nicht zu zweifeln. Die Rippen sind schmal, sehr erhaben, und zu beiden Seiten gehen in den Furchen eigentümliche Zähnchen herab, die sich nicht berühren. Nur in der Jugend scheinen diese Zähnchen wie bei *subpunctatus* die ganze Furche zu füllen.'

2. AMENDED DIAGNOSIS

Distinguished from all other species of *S. (Spondylopecten)* by the number of plicae (42–48).

3. AMENDED DESCRIPTION

Essentially similar to *S. (S.) subpunctatus*. Differing by the diagnostic larger number of plicae (see Section 2), whose range of variation, if anything, increases phyletically (see Section 10) and by the generally higher umbonal angle, whose range of variation is from 91° (BM 66825) to 107° (BM L84341).

There is insufficient data to chart phyletic changes in umbonal angle and convexity; C/H for Bajocian forms is plotted in text fig. 87.

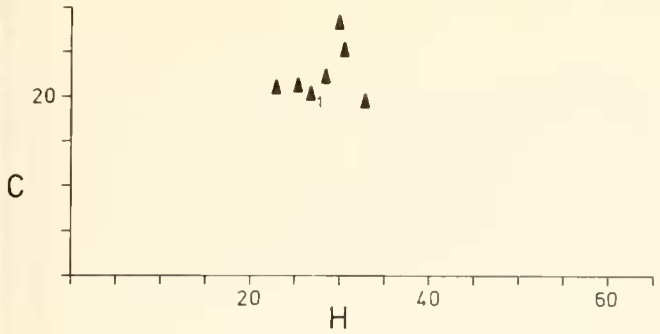
The maximum height is 33.5 mm (BM L41934).

4. DISCUSSION

The original description of '*P.*' *cardinatus* Quenstedt (see Section 1) does not specify the number of plicae but the figure shows about 36, which suggests that it might be an extreme representative of *S. (S.) subpunctatus*. There seem to be no traces of the original to the figure (or of any other type specimens) in the Quenstedt Collection (GPIT) and it may be lost. However, Staesche (1926) probably had access to the specimen and applied the name to forms with about 45 plicae, as in the species described in Section 3. If it could be established beyond reasonable doubt that Quenstedt's type material is lost the most sensible course would be to designate a neotype in conformity with Staesche's hypodigm. Until this is done the species described in Section 3 can only provisionally be accorded the name *S. (S.) cardinatus*.

The sole observed syntype of '*P.*' *spinicostatus* Whidborne (BM 66825; Pl. 3, Fig. 21) possesses about 45 plicae and in its convexity (1) and number of spine rows (2) is indistinguishable from *S. (S.) cardinatus*.

Of the specimens which Yin (1931) placed in '*P.*' *cordiformis* Gemmellaro and Di Blasi, only one, with 60 plicae, is referable to that species (= *S. (S.) globosus*). The remainder, with 42–48 plicae, are inseparable from *S. (S.) cardinatus*.



Text fig. 87: *Spondylopecten (S.) cardinatus* – convexity/height.

5. STRATIGRAPHIC RANGE

Although a long-lived species *S. (S.) cardinatus* is only known from a few disjunct records. The earliest is from the Parkinsoni zone (U. Bajocian) of the Cotswolds where at least seven specimens (see Section 7) have been found. Staesche (1926) states that the species occurs sporadically in the Oxfordian and Kimmeridgian of S. Germany but it would seem that only two specimens have actually been recovered, one from the U. Oxfordian (GPIT) and one from the Kimmeridgian (Staesche's measured specimen). A further two specimens (GPIT, BM 49199) are known from the L. Tithonian of the same area. 15 specimens are recorded from the U. Tithonian of S. France (Yin, 1931).

6. GEOGRAPHIC RANGE

S. (S.) cardinatus is unknown outside Europe. Within Europe, records are widespread but patchy (see Section 5). They seem to indicate a gradual southward migration.

7. DESCRIPTION OF ECOLOGY

S. (S.) cardinatus is found in the U. Coral Bed (U. Bajocian) at Dundry nr. Bristol and its probable lateral equivalent at Cleeve Cloud nr. Cheltenham (assoc. fauna p. 95). Seven specimens are contained in the BM, three with 43 plicae, three with 44 and one with 46. The maximum height is 33.5 mm (BM L41934).

Specimens from the Oxfordian and Kimmeridgian of S. Germany (see Section 5) are, according to Staesche (1926), derived from sponge 'reef' facies (fauna p. 101). Staesche cites a height of 31 mm for a Kimmeridgian specimen. Specimens from the L. Tithonian of Nattheim (Swabian Alb) and from the U. Tithonian of Languedoc (see Section 5) are derived from coral reef facies (fauna p. 88) and have a range of plical variation from 42–48. The largest known specimen has a height of about 25 mm (BM 49199).

8. INTERPRETATION OF ECOLOGY

It is apparent from Section 7 that coralliferous deposits constituted the most favourable environment for *S. (S.) cardinatus*. Both short-lived coral stands and reefs seem to have been suitable (cf. Hertlein, 1969; Hallam, 1976) although by no means all such coral accumulations were colonised. In particular, the absence of *S. (S.) cardinatus* from the coralliferous deposits in the Oxfordian of England and E. France, the Oxfordian and Kimmeridgian of the Jura, and the Tithonian of the Franconian Alb, Czechoslovakia and Sicily, is very noticeable. An explanation in terms of the general structure of the coral accumulations (see p. 88) is precluded by the presence of other *Spondylopecten* species and the invocation of interspecific competition (see p. 101) does nothing to solve the problem since at one time or another *S. (S.) cardinatus* occurs with abundant examples of each of the other *S. (Spondylopecten)* species (e. g. with *S. (S.) palinurus* in the U. Bajocian of England, with *S. (S.) subpunctatus* in the U. Tithonian of France and with *S. (S) globosus* in the L. Tithonian of S. Germany). A highly specific commensal relationship (see p. 96) seems to be ruled out by the fact that *S. (S.) cardinatus* was apparently able to colonise sponge as well as coral accumulations and a temperature control can be discounted because the distribution of the species is still inconsistent in coralliferous deposits at the same palaeolatitude (e. g. in the S. German Tithonian).

9. FUNCTIONAL MORPHOLOGY

As for other species of *S. (Spondylopecten)* little can be added to the general interpretation of functional morphology presented for the genus as a whole (p. 89). The considerable variation in convexity of *S. (S.) cardinatus* is further suggestive of a 'wedged' mode of life. The comparable mean convexity to that of both *S. (S.) palinurus* and *S. (S.) subpunctatus* suggests that cavities of the order of size occupied by these species were also colonised by *S. (S.) cardinatus*.

The small maximum height (33.5 mm) indicates that *S. (S.) cardinatus* could have remained byssate throughout ontogeny (see p. 101) and it is likely that, even if it did unattach itself, swimming would have been severely restricted by the inflated form.

10. ORIGINS AND EVOLUTION

Assuming that *S. (S.) subpunctatus* arose in the Aalenian (see p. 100) the latter is the most likely ancestor for *S. (S.) cardinatus*. Otherwise the only possible ancestor within the subgenus is *S. (S.) palinurus*. In neither case could trans-specific evolution have been based on heterochrony so some major change in the genome is implied. There is no evidence that this occurred gradually.

There is too little data to allow a confident assertion of the existence of phyletic evolution within *S. (S.) cardinatus*. However a slight phyletic increase in the range of plical variation (from 43–46, U. Bajocian to 42–48, U. Tithonian) and a decrease in maximum height (from 33.5 mm, U. Bajocian to 31 mm, Kimmeridgian to about 25 mm, U. Tithonian) is indicated by the few available specimens. Both trends would seem to indicate 'r' selection (Gould, 1977) in contrast to the apparent field occurence of the species, as a fairly rare element in high diversity faunas (see Section 7), which suggests the prevalence of 'K' selection.

Spondylopecten (Spondylopecten) globosus (QUENSTEDT 1843)

Pl. 3, Figs. 22–24; text fig. 88

Synonymy

pv* 1843	*Pecten globosus* sp. nov; QUENSTEDT, p. 476.
v* 1852	*Pecten globosus* QUENSTEDT; QUENSTEDT, p. 507, pl. 40, fig. 46 (non fig. 45).
v* 1858	*Pecten globosus* QUENSTEDT; QUENSTEDT, p. 755, pl. 92, fig. 20 (non pl. 78, fig. 2).
non 1862	*Pecten Globosus* QUENSTEDT; THURMANN and ÉTALLON, p. 250, pl. 35, fig. 1.
non 1867	*Pecten globosus* QUENSTEDT; DE LORIOL, p. 335, pl. 13, fig. 3.
1874	*Pecten cordiformis* sp. nov; GEMMELLARO and DI BLASI, p. 108, pl. 2, figs. 11–15.
1875	*Pecten cordiformis* GEMMELLARO and DI BLASI; GEMMELLARO, p. 43.
1883	*Pecten cordiformis* GEMMELLARO and DI BLASI; BOEHM, p. 611, pl. 67, figs. 27–29.
1883	*Spondylus globosus* (QUENSTEDT); BOEHM, p. 644, pl. 70, figs. 3, 4.
? 1893	*Pecten globosa* QUENSTEDT; SIEMIRADZKI, p. 119.
non 1898	*Pecten (Spondylopecten) globosus* QUENSTEDT; PHILIPPI, p. 620, text figs. 6, 7.
1898	*Spondylopecten G. Boehmi* sp. nov; PHILIPPI, p. 620.
1903	*Pecten cordiformis* GEMMELLARO and DI BLASI; REMES, p. 202, pl. 29, fig. 6.
1903	*Pecten G. Boehmi* PHILIPPI; REMES, p. 205.
non 1903	*Pecten (Spondylopecten) globosus* QUENSTEDT; REMES, p. 205.
? *1905*	*Pecten (Chlamys) globosus* QUENSTEDT; KILIAN and GUEBHARD, p. 817.
1910	*Pecten globosus* QUENSTEDT; LISSAJOUS, p. 362, pl. 10, fig. 5.
non 1913	*Pecten globosus* QUENSTEDT; JOUKOWSKY and FAVRE, p. 40, pl. 17, figs. 3–6.
1920	*Pecten cordiformis* GEMMELLARO and DI BLASI; FAURE-MARGUERIT, p. 57.
non 1920	*Pecten (Spondylopecten) globosus* QUENSTEDT; FAURE-MARGUERIT, p. 60.
1926	*Spondylopecten globosus* (QUENSTEDT); STAESCHE, p. 110.
non 1931	*Pecten (Spondylopecten) globosus* QUENSTEDT; YIN, p. 118, pl. 12, figs. 3–6.
p 1931	*Pecten cordiformis* GEMMELLARO and DI BLASI; YIN, p. 119, pl. 12, fig. 7, pl. 13, fig. 7.
1936	*Spondylopecten globosus* (QUENSTEDT); DECHASEAUX, p. 66.
? *1959*	*Spondylopecten globosus* (QUENSTEDT); HÖLDER and ZIEGLER, p. 165.
v 1975	*Spondylopecten globosus* (QUENSTEDT); YAMANI, p. 62, pl. 3, figs. 7–9.

Lectotype of *Pecten globosus* QUENSTEDT 1843, p. 476 designated herein; GPIT 2–40–46; figured QUENSTEDT, 1852, pl. 40, fig. 46, 1858, pl. 92, fig. 20; Pl. 3, Figs. 22, 23 herein; H: 23, L: 25, AH: 7.5, PH: 5.5, I: 16, C: 24, UA: 94, PL: 63; Malm ε (L. Tithonian; see p. 105), Nattheim, Swabia.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

‚Beide Schalen sind aufgebläht, wie die gewölbte Schale des *P. gryphaeatus* der Kreide, und nähern sich insofern aufeinander geklappt der Kugelform, die Rippen markiert und nie dichotum, große Symmetrie, wie bei *Pectunculus*, auch stehen die Wirbel weit voneinander. Dem *Pecten subpunctatus* sehr verwandt, nur werden sie viel größer.

Bemerkenswert sind die Formen welche dem *Pecten aequicostatus* Sow. (*gryphaeatus* Schl.) gleichen, und die namentlich im weißen Korallenkalke von Arnegg wie von Au bei Kelheim in so großer Häufigkeit vorkommen. Auch in den kieseligen Kalken von Nattheim fehlen sie nicht, und auffallenderweise erheben sich neben dem deltaförmigen Schloßmuskelloch zwei Zähne, von denen besonders der vordere sehr lange und kräftig wird.‘

2. AMENDED DIAGNOSIS

Distinguished from all other species of *S. (Spondylopecten)* by the number of plicae (51–71).

3. AMENDED DESCRIPTION

Essentially similar to *S. (S.) cardinatus*. Differing by the diagnostic larger number of plicae (see Section 2), whose median value, if anything, oscillates phyletically (see Section 10), and by the generally lower umbonal angle and higher convexity. There is insufficient data from which to accurately assess the range of variation in the latter parameters. The lectotype of the species (see above) probably exhibits fairly typical proportions. The maximum height is 26.9 mm (STAESCHE, 1926).

4. DISCUSSION

QUENSTEDT's (1843) original hypodigm for '*P.*' *globosus* is a matter of some doubt. A comparison with '*P.*' *subpunctatus* MÜNSTER combined with a reference to very high convexity in the original description (see Section 1) suggests that it included forms referable to both *S. (S.) subpunctatus* and the species described in Section 3. This interpretation is borne out by the fact that the QUENSTEDT Collection (GPIT) used to contain two specimens labelled '*P.*' *globosus*, one with moderate convexity and about 30 plicae and the other with high convexity and about 60 plicae, and by the fact that both specimens were figured by QUENSTEDT as '*P.*' *globosus* in later works (1852, 1858). For the purposes of this work it is desirable to restrict QUENSTEDT's taxonomic species by designating one or other specimen as the lectotype. However, following Recommendation 74A of the ICZN (N. R. STOLL et al., 1964) due weight is given in the choice to valid restrictions of the species by previous authors, as discussed below.

THURMANN and ÉTALLON (1862), DE LORIOL (1867), JOUKOWSKY and FAVRE (1913), PHILIPPI (1898), REMES (1903), FAURE-MARGUERIT (1920) and YIN (1931) all apply QUENSTEDT's specific name to forms with about 30 plicae (see p. 99). However, only in the last four cases is it clear, from the fact that other specimens with about 60 plicae are referred to different species, that these authors actually restricted their concept of QUENSTEDT's taxonomic species to forms with about 30 plicae. In fact, PHILIPPI's citation of the specimen figured in pl. 92, fig. 20 of Der Jura (the form with about 60 plicae) as type for his restricted concept of the species effectively re-expands his hypodigm to that probably envisaged originally by QUENSTEDT.

Boehm (1883), Lissajous (1910), Staesche (1926), Dechaseaux (1936) and Yamani (1975) apply Quenstedt's specific name to forms with about 60 plicae. All but Lissajous give a clear indication that their concept of Quenstedt's taxonomic species is restricted to such forms by referring other specimens with about 30 plicae to different species. Staesche suggests moreover that Quenstedt himself may have intended such a restriction in Der Jura. It is Staesche's contention that in the latter work (1858), in which *'P.' aequatus*, a new species with about 30 plicae is also figured, Quenstedt applied the name *'P.' globosus* by mistake to an illustration of the cardinal area of a form with about 30 plicae which he really meant to label as a second figure of *'P.' aequatus*. On these grounds Staesche draws the logical conclusion that in 1858 Quenstedt restricted his hypodigm for *'P.' globosus* to forms with about 60 plicae. There is however no a priori reason to think that Quenstedt made a nomenclatural error and furthermore there are no grounds for believing, as Staesche seems to imply, that Quenstedt intended such a restriction all along. The description in 1843 and the illustrations in 1852 belie this reasoning (see above). On the available evidence one must draw the conclusion that Quenstedt erected *'P.' aequatus* as a species distinct from the original specimen of *'P.' globosus* with about 30 plicae.

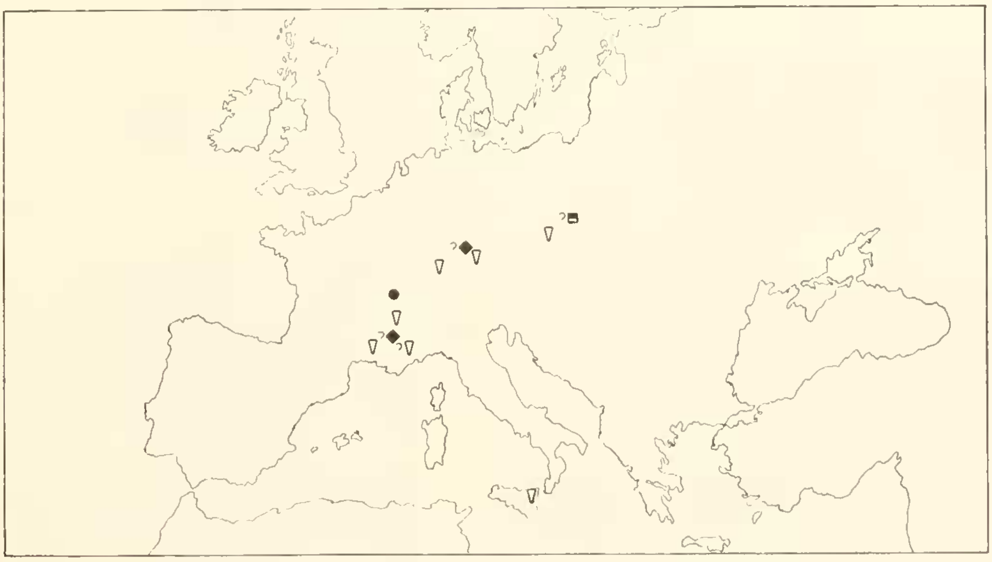
In summary it can be said that previous restricted usage of Quenstedt's taxonomic species is, on the basis of specimens described in the literature studied by the author, apparently equally divided between forms with about 30 and forms with about 60 plicae. Weight of numbers therefore gives no lead in the selection of an appropriate lectotype for *'P.' globosus*. The first author to apply Quenstedt's specific name in a clearly restricted sense was Boehm (1883) who used the name for forms with about 60 plicae. Therefore on grounds of historical precedence the original specimen with about 60 plicae is the most appropriate choice for the lectotype of *'P.' globosus*. Since this specimen appears to be the only one remaining of the two originally housed in the GPIT such a selection also avoids any possible need to designate a neotype. Accordingly the specimen with about 60 plicae (Pl. 3, Figs. 22, 23) is herein designated as lectotype. As a result *Spondylopecten G. Boehmi* Philippi, which was erected for this and another specimen (following restriction of Quenstedt's taxonomic species to the original specimen with about 30 plicae), would seem to become a junior objective synonym, and if so must be rejected.

Non-synonymous and questionably synonymous usages of Quenstedt's specific name quoted in the synonymy are discussed on p. 99. All other usages are within the present author's hypodigm for *S. (S.) globosus* (see Section 3).

'P.' cordiformis Gemmellaro and Di Blasi is inseparable from *S. (S.) globosus* by its inflation (C/L: 0.94) and number of plicae (56). Nevertheless Boehm (1883) considered that the two species should be placed in separate genera (*cordiformis* in *Pecten*, *globosus* in *Spondylus*) on the basis of the lack of a cardinal area in the former and of a byssal notch in the latter. However, Staesche (1926) has pointed out that this is merely the result of poor preservation and that therefore the species cannot be separated at any level. Of the forms referred to Gemmellaro and Di Blasi's species by Yin (1931) only one, with 60 plicae, is referable to *S. (S.) globosus*. The remainder, with 42–48 plicae, must be assigned to *S. (S.) cardinatus*.

5. STRATIGRAPHIC RANGE

An indeterminate number of specimens from the U. Oxfordian of the Mâconnais (Lissajous, 1910; Dechaseaux, 1936) constitutes the first certain record of *S. (S.) globosus*. Yamani (1975) states that the species occurs in the Callovian of S. France but provides no evidence in the form of a reference. His record of the species from the Kimmeridgian of S. Germany is also doubtful since it is probably based on Quenstedt's (1843) description of *'P.' globosus* from Kelheim (see Section 1), which may in fact refer to *S. (S.) subpunctatus* (see Section 4). No museum specimens of *S. (S.) globosus* are known from the latter locality but examples of *S. (S.) subpunctatus* are quite common. A specimen of *S. (S.) globosus* labelled 'Malm ε , Ulm' in the GPIT could well be from the L. Tithonian rather than the Kimmeridgian, as the



Text fig. 88: *Spondylopecten (S.) globosus* – European distribution.

label implies. Museum specimens from the L. Tithonian reef facies in S. Germany are invariably incorrectly labelled in this way. Since the only other record of Kimmeridgian *S. (S.) globosus* (Holder and Ziegler, 1959) is of questionable validity (see p. 99) there are no unequivocal occurrences of the species in the stage.

S. (S.) globosus becomes locally common in the L. Tithonian and continues thus into the U. Tithonian (Gemmellaro and Di Blasi, 1874; Gemmellaro, 1875; Boehm, 1883; Faure-Marguerit, 1920; Yin, 1931).

6. GEOGRAPHIC RANGE

S. (S.) globosus is unknown outside Europe. Within Europe (text fig. 88) the species is restricted to the central and southern parts of the continent, where its local distribution is intimately linked with that of coralliferous deposits (see Sections 7, 8).

7. DESCRIPTION OF ECOLOGY

The records of *S. (S.) globosus* from the U. Oxfordian of the Mâconnais (see Section 5) are from coralliferous limestones. The range of plical variation is apparently from 55–65 (Dechaseaux, 1936).

In the L. Tithonian *S. (S.) globosus* is reported to be common in the coral reefs at Nattheim, Sirchingen and Wittlingen in Swabia (Staesche, 1926) and to also occur in the same facies at Neuburg in Franconia (Yamani, 1975). The range of plical variation is from 51 (GPIT) – 65 (Staesche, 1926) and the maximum height is 26.9 mm (Staesche, 1926). The species is also known from coral reef facies in the U. Tithonian of S. France (Faure-Marguerit, 1920; Yin, 1931), Sicily (Gemmellaro and Di Blasi, 1874; Gemmellaro, 1875) and Czechoslovakia (Boehm, 1883; Remes, 1903) where it is particularly abundant and reaches a maximum height of 24 mm (BM L23886). The range of plical variation in U. Tithonian forms is from 56 (Gemmellaro and Di Blasi, 1874) to 71 (BM LL17205). The typically associated fauna in Tithonian occurrences of *S. (S.) globosus* is described on p. 88.

There are no certain occurrences of *S. (S.) globosus* apart from those discussed above.

8. INTERPRETATION OF ECOLOGY

It is clear from Section 7 that *S. (S.) globosus* was a coral reef-dwelling species. However, by no means all such reefs were colonised. The absence of the species from reef and reef-derived sediments in the Oxfordian of England, N. France and N. Germany (see Section 6) could perhaps be the consequence of a temperature restriction. However, the inconsistent distribution in coral reefs at approximately the same palaeolatitude (presence in the Tithonian of Czechoslovakia and S. Germany, absence from the Oxfordian of the E. Paris Basin, Oxfordian and Kimmeridgian of the Jura, Kimmeridgian of La Rochelle and probably also Kelheim) argues against this hypothesis. While the general reef structure might be the cause of the lack of *S. (S.) globosus* at La Rochelle (see p. 88) it cannot be invoked as an explanation for absences from the other reefs, in each of which at least one of the other *S. (Spondylopecten)* species is known to occur commonly. Competitive exclusion by *S. (S.) palinurus* is another possible explanation since the latter is present at all of the above localities where *S. (S.) globosus* is absent, apart from Kelheim. Moreover, the two species are not known to occur together in large numbers at any locality. However, if *Spondylopecten* species occupied different microhabitats (see p. 89) it seems unlikely that they would have competed and indeed there is little evidence of competition in general (see p. 103). An alternative explanation for the distribution of *S. (S.) globosus* in terms of a commensal relationship with one particular coral species must also be considered doubtful on the basis of the failure of such a hypothesis (see p. 96) to account for the irregular distributions of other *S. (Spondylopecten)* species. There is, however, no specific reason for rejection in the case of *S. (S.) globosus*.

9. FUNCTIONAL MORPHOLOGY

Little can be added to the general interpretation of functional morphology in *Spondylopecten* presented on p. 89.

The maximum height of 26.9 mm indicates that the species could have remained byssate throughout ontogeny (see p. 101) while the inflated form renders it likely that if it unattached itself at all, *S. (S.) globosus* could only have been a very inefficient swimmer.

Such phyletic changes in height and plical variation as may have occurred (see Section 10) are too small to have had any effect on the mechanics of the shell (cf. pp. 97, 101).

10. ORIGINS AND EVOLUTION

The most likely ancestor for *S. (S.) globosus* is *S. (S.) cardinatus*. A 'genetic revolution' presumably accompanied speciation since the lack of ancestral allometry rules out evolution by heterochrony. There is no evidence that speciation occurred gradually, but some suggestion that it occurred, at least on a small scale, allopatrically, since the first occurrence of *S. (S.) globosus* is as an isolated population (U. Oxfordian, Mâconnais) apparently at the edge of the contemporaneous geographic range of *S. (S.) cardinatus*.

The apparent phyletic oscillation in the median number of plicae (60, U. Oxfordian; 58, L. Tithonian; 63/64, U. Tithonian) may well be more a consequence of the limited number of museum specimens available to the author than a reflection of a real phenomenon.

Museum specimens indicate no significant change in maximum height in the passage from L. (26.9 mm) to U. (24 mm) Tithonian.

Genus *CAMPTONECTES* Agassiz in Meek 1864

Type species. SD; Stoliczka 1871, p. 425; *Pecten lens* J. Sowerby 1818, p. 3, pl. 205, figs. 2, 3; Corallian Beds (Oxfordian) of the Oxford district.

AMENDED DIAGNOSIS

Part or all of exterior ornamented with fine, oblique, divergent, curved, crenulated, commonly punctate striae and concentric lines or raised laminae. L. Jur. – U. Cret., cosmop.

DISCUSSION

Hertlein's (1969: N351) diagnosis for *Camptonectes* has been slightly altered so as to expressly include forms (e. g. *C. (C.) subulatus*, *C. (Camptochlamys) clathratus*) which only have the distinctive divaricate ornament on a small part of the shell. Such forms are undoubtedly related to the more typical members of the genus well provided with divaricate ornament. Examples of *C. (C.) subulatus* which possess only a small byssal notch (e. g. Pl. 4, Fig. 7) closely resemble the contemporaneous species *Entolium (E.) lunare*. They may, however, be distinguished by the features described on p. 35 thus there is little evidence to support Staesche's (1926: 55) contention that *Camptonectes* and *Entolium* are convergent in the L. Jurassic.

Subgenus *CAMPTONECTES* s. s.

(Errors *Campstonectes* von Teppner 1922 [nom. null.]
Campitonectes Salisbury 1939 [nom. null.]
Camponectes Vyalov and Korobkov 1939
[nom. null.])

AMENDED DIAGNOSIS

Concentric sculpture of fine growth lines. L. Jur. (Hettang.) – U. Cret. (Maastricht.), cosmop.

DISCUSSION

In his diagnosis,Hertlein (1969: N351) stated that the first occurrence of *C. (Camptonectes)* was in the U. Lias (Toarcian). *C. (C.) subulatus* and *C. (C.) auritus* are known, however, from the lowermost horizons in the Lias.

In well preserved material four groups may be distinguished in Jurassic *C. (Camptonectes)* on the following basis:

1. Sub-ovate disc, fine divaricate striae on all parts of disc (= *C. (C.) virdunensis*).
2. Sub-orbicular disc, fine divaricate striae on all parts of disc 6= *C. (C.) auritus*).
3. Sub-orbicular disc, coarse divaricate striae on all parts of disc (= *C. (C.) laminatus*).
4. Sub-orbicular disc, fine divaricate striae restricted to anterior and posterior margins of disc (= *C. (C.) subulatus*).

As pointed out by Arkell (1930a), Group 3 may also be distinguished from Group 2 by the presence of comarginal lamellae on the anterior auricle of the left valve. Contrary to Arkell's opinion lamellae are not consistently developed on the posterior auricle of the right valve in Group 3 and it is not possible to distinguish the two groups on the basis of H/L (text figs. 98, 108) or H/UA (text figs. 99, 109). Group 3 almost entirely replaces Group 2 in the Bathonian of Europe yet there are no certain records of Group 2 elsewhere to evince a migration. The possibility therefore that the coarser ornament distinguishing Group 3 is merely an ecophenotypic response of Group 2 to Bathonian environments cannot be entirely discounted. An analysis along the lines adopted for *Radulopecten vagans* (see Johnson, 1981) could be used to text this hypothesis. However, until this is undertaken it seems preferable to treat the two groups as separate species. A similar approach is taken for Group 1, in which the high H/L (text fig. 118) and H/UA (text fig. 119) might merely be an ecophenotypic response of Group 2 to the coral reef habitat. Recent species from such environments often take on an elongated shape as the result of the physical restriction on growth imposed by a dense coral framework (Waller, 1972b).

Although within Group 2 there are systematic variations in metric proportions with horizon and geography these are more easily interpreted as an expression of respectively phyletic evolution and ecophenotypic variation (see p. 117) in a single species rather than as a result of the existence of numerous species within Group 2.

Camptonectes (Camptonectes) subulatus (Münster 1836)

Pl. 4, Figs. 3–5, 7, 8, ?Figs. 6, 9; text figs. 89–97

Synonymy

? 1833	*Pecten textilis* sp. nov; Münster in Goldfuss, p. 43, pl. 89, figs. 3a–d.
1836	*Pecten subulatus* sp. nov; Münster in Goldfuss, p. 73, pl. 98, figs. 12a–c.
v* 1836	*Pecten calvus* sp. nov; Goldfuss, p. 74, pl. 99, figs. 1a–c.
1836	*Pecten substriatus* sp. nov; Roemer, p. 71.
? 1839	*Pecten dextilis* Münster; Roemer, p. 28, pl. 28, figs. 24a–c.
v* 1850	*Pecten Castor* sp. nov; d'Orbigny, v. 1, p. 220 (Boule, 1907, v. 2, p. 167, pl. 23, fig. 15).
(?) *1850*	*Pecten subulatus* Münster; d'Orbigny, v. 1, p. 257.
(?) *1850*	*Pecten calvus* Goldfuss; d'Orbigny, v. 1, p. 257.
? 1858	*Pecten amatus* sp. nov; Andler, p. 644.
v*? 1858	*Pecten disparilis* sp. nov; Quenstedt, p. 47, pl. 4, figs. 8, 9.
v* 1858	*Pecten punctatissimus* sp. nov; Quenstedt, p. 79, pl. 9, fig. 14.
v* 1858	*Pecten strionatis* sp. nov; Quenstedt, pp. 147, 183, pl. 18, fig. 21, pl. 23, fig. 2.
? 1858	*Pecten Trigeri* sp. nov; Oppel, p. 103.
1863	*Pecten subulatus* Münster; Schlönbach, p. 544.
? 1865	*Pecten punctatissimus* Quenstedt; Terquem and Piette, p. 103, pl. 12, fig. 62.
1865	*Pecten jamoignensis* sp. nov; Terquem and Piftte, p. 104, pl. 12, figs. 20, 21.
v*? 1866	*Pecten Etheridgii* sp. nov; Tawney, p. 81, pl. 3, fig. 4.
1870	*Pecten Lohbergensis* sp. nov; Emerson, p. 318, pl. 9, figs. 4, 4a, 4b.
(?) 1871	*Pecten subulatus* Münster; Brauns, p. 393.
(?) 1876	*Pecten calvus* Goldfuss; Tate and Blake, p. 362.
(?) 1876	*Pecten punctatissimus* Quenstedt; Tate and Blake, p. 362.
1876	*Pecten Lohbergensis* Emerson; Tate and Blake, p. 362.
(?) 1876	*Pecten substriatus* Roemer; Tate and Blake, p. 362.
1878	*Pecten (Amusium) Bellampensis* sp. nov; Gemmellaro and Di Blasi, p. 403, pl. 30, figs. 15, 16.
1881	*Pecten Tullbergi* sp. nov; Lundgren, p. 28, pl. 5, figs. 11, 12.
v* 1884	*Pecten punctatus* sp. nov; Simpson, p. 171.
? 1888	*Pecten Lundgreni* sp. nov; Moberg. p. 35, pl. 1, figs. 27–32.

(?) 1888 *Pecten subulatus* Münster; Moberg, p. 36, pl. 1, fig. 33.
1895 *Pecten Rinki* sp. nov; Lundgren, p. 200, pl. 3, fig. 14.
? 1906 *Pecten* cfr. *Bellampensis* Gemmellaro and Di Blasi; Fucini, p. 617, pl. 11, fig. 1.
(?) 1907 *Pecten (Entolium?) calvus* Goldfuss; Joly, p. 76.
1907 *Pecten (Entolium?) jamoignensis* Terquem and Piette; Joly, p. 76.
1909 *Pecten (Chlamys) subulatus* Münster; Trauth, p. 90.
(?) 1916 *Pecten strionatis* Quenstedt; Jaworski, p. 417.
? 1917 *Pecten tingensis* sp. nov; Tilmann, p. 674, pl. 24, fig. 6.
v* 1923 *Pecten dehmensis* sp. nov; Ernst, p. 54, pl. 1, figs. 10, 11.
1923 *Pecten (Pleuronectites) sublaevigatus* sp. nov; Ernst, p. 57, pl. 1, fig. 9.
1926 *Chlamys (Camptonectes?)* cf. *lohbergensis* (Emerson); Cox, p. 180.
? 1926 *Chlamys Trigeri* (Oppel); Staesche, p. 56.
v 1926 *Chlamys subulata* (Münster); Staesche, p. 57, pl. 2, figs. 9, 10, pl. 5, fig. 6.
v non 1926 *Chlamys calva* (Goldfuss); Staesche, p. 58, pl. 2, figs. 11, 12.
? 1926 *Chlamys substriata* (Roemer); Staesche, p. 63.
1926 *Chlamys punctatissima* (Quenstedt); Staesche, p. 73.
v 1926 *Camptonectes* aff. *sublaevigato* (Ernst); Staesche, p. 75, pl. 3, figs. 1, 8, 11.
(?) 1928 *Chlamys substriata* (Roemer); Cox, p. 242.
v 1934 *Chlamys substriata* (Roemer); Kühn, p. 472, pl. 18, figs. 6a, 6b.
(?) *1934* *Chlamys substriata* var. *rinki* (Lundgren); Rosenkrantz, p. 113.
1934 *Camptonectes* aff. *sublaevigatus* (Ernst); Rosenkrantz, p. 117.
v 1935 *Chlamys substriata* (Roemer); Kühn, p. 246, pl. 12, fig. 35.
1936 *Pecten (?Chlamys) jamoignensis* Terquem and Piette; Dechaseaux, p. 28.
1936 *Pecten (?Chlamys) subulata* Münster; Dechaseaux, p. 28.
(?) 1936 *Chlamys ? punctatissimus* (Quenstedt); Dechaseaux, p. 29.
v 1936 *Camptonectes* sp; Dechaseaux, p. 29, pl. 4, figs. 7, 8.
(?) *1942* *Chlamys substriata* var. *rinki* (Lundgren); Rosenkrantz, pp. 23, 29, 30, 32, 38.
1948 *Pecten (Camptonectes)* sp; Dubar, p. 161, pl. 13, fig. 2.
1951 *Chlamys subulata* (Münster); Troedsson, p. 212, pl. 20, fig. 17.
1951 *Chlamys tullbergi* (Lundgren); Troedsson, p. 213, pl. 23, figs. 5, 6.
non 1951 *Entolium calvum* (Goldfuss); Troedsson, p. 217, pl. 20, figs. 9–13.
non 1951 *Entolium lundgreni* (Moberg); Troedsson, p. 218, pl. 20, figs. 4–8.
1956 *Chlamys subulata* (Münster); Melville, p. 121, pl. 5, fig. 3.
non 1956 *Chlamys subulata securis* (Dumortier); Melville, p. 121, pl. 5, figs. 4, 5.
1956 *Chlamys ?calva* (Goldfuss); Melville, p. 122, pl. 5, figs. 1, 2.
1956 *Camptonectes jamoignensis* (Terquem and Piette); Melville, p. 123.
1956 *Camptonectes lohbergensis* (Emerson); Melville, p. 123, pl. 5, fig. 6.
v 1956 *Camptonectes mundus* sp. nov; Melville, p. 124, pl. 1, figs. 1–4.
1963 *Camptonectes lohbergensis* (Emerson); Hallam, p. 561.
(?) *1966* *Entolium* cf. *subulatum* (Münster); Behmel and Geyer, p. 26.
1967 *Camptonectes lohbergensis* (Emerson); Berridge and Ivimey-Cook, p. 160.
1967 *Camptonectes mundus* Melville; Berridge and Ivimey-Cook, p. 160.
(?) *1967* *Chlamys subulata* (Münster); Berridge and Ivimey-Cook, p. 160.
(?) *1968* *Chlamys (?) calva* (Goldfuss); Wobber, p. 306.
(?) *1968* *Chlamys subulata* (Münster); Wobber, p. 306.
(?) *1971* *Chlamys subulata* (Münster); Hallam, pp. 242, 243.
? 1972 *Camptonectes (Camptonectes) fromageti* sp. nov; Hayami, p. 195, pl. 34, figs. 5–8.

No trace of the type material of *Pecten subulatus* Münster in Goldfuss 1836, p. 73, pl. 98, figs. 12a–c has yet been found in the Münster/Goldfuss Collections in BSPHG and GPIB. The material was derived from the 'Liaskalk' (L. Jurassic) of S. Germany.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

'Pecten testa oblique ovali aequivalvi inaequilaterali convexo-plana laevi, striis radiantibus et concentricis vix conspicuis, auricula antica elongata basique sinuata.

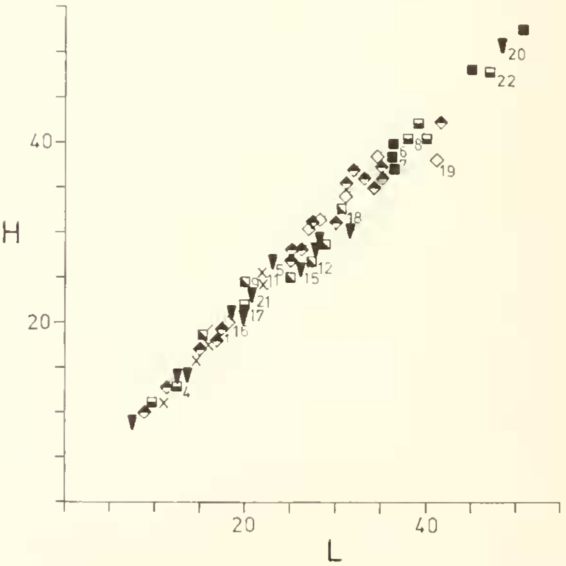
E montibus Bavaricus et Wurtembergicis M. M.

Gleichklappig, schief oval-kreisrund, flach-convex, glatt und glänzend. Durch Vergrößerung erkennt man sehr zarte, gedrängte konzentrische Streifen und einige ausstrahlende Linien. Die Ohren sind in etwas abweichender schiefer Richtung abgeschnitten, die hintern sehr kurz, die vordern aber weit über den Rand hinaus verlängert.

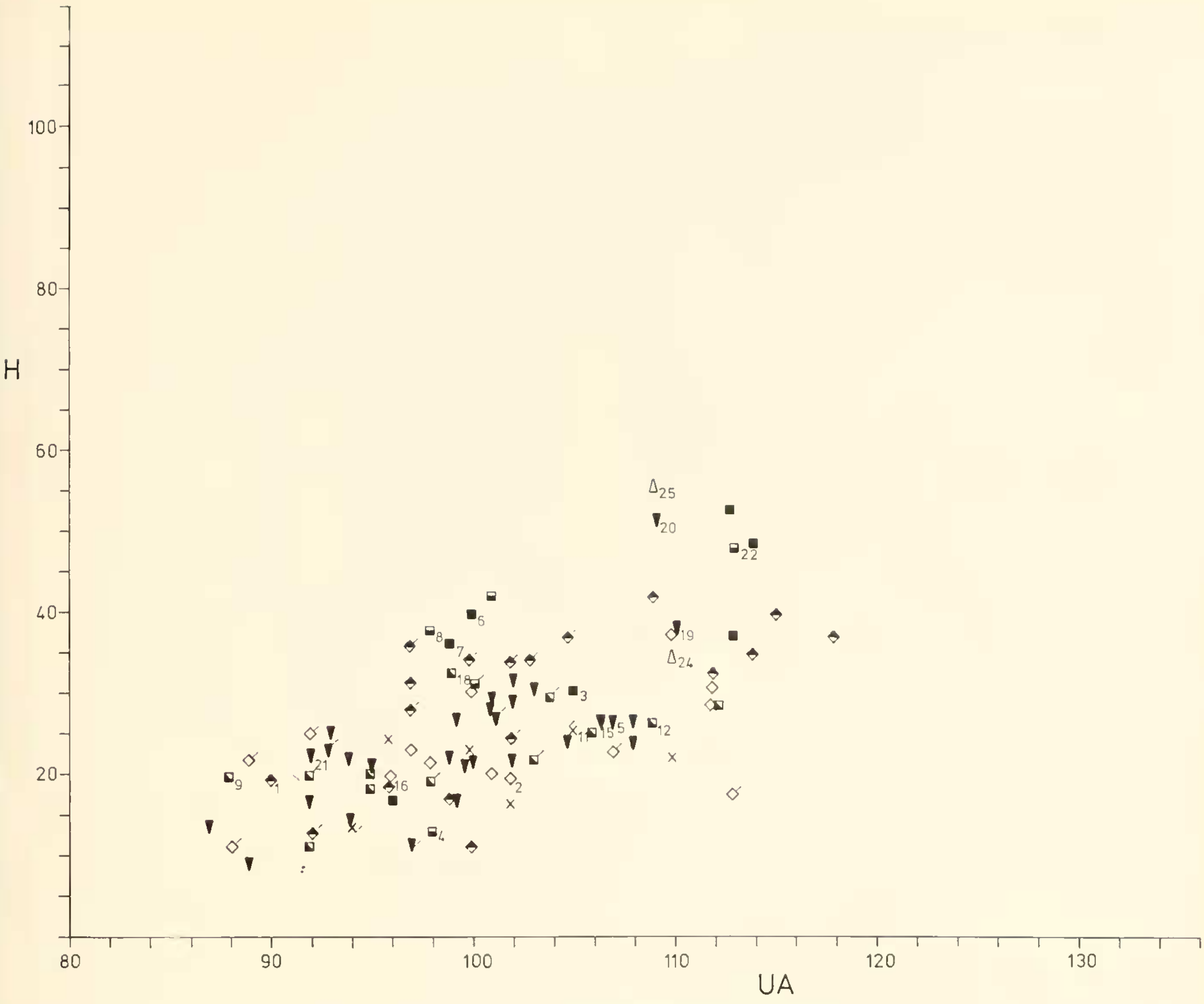
Findet sich im Liaskalk bei Altdorf, Amberg, Ellwangen und Wasser-Alfingen.'

2. AMENDED DIAGNOSIS

Distinguished from *C. (C.) auritus* and *C. (C.) laminatus* by the restriction of surficial ornament to the anterior and



Text fig. 89: *Camptonectes (C.) subulatus* – height/length.



Text fig. 90: *Camptonectes (C.) subulatus* – height/umbonal angle.

posterior margins. Distinguished from *C. (C.) virdunensis* by the more orbicular disc.

3. AMENDED DESCRIPTION

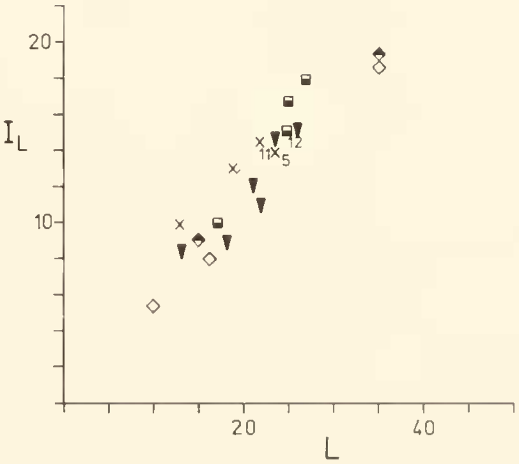
Disc sub-orbicular, slightly higher than long at all stages in ontogeny (text fig. 89); maximum height 52.5 mm (GPIT). Umbonal angle very variable (text fig. 90) but increasing during ontogeny to produce concave dorsal margins. Disc flanks very low.

Equilateral; inequivalve, low convexity, left valve slightly more convex than right.

Intersinal distance variable, greater in left valve than right (text figs. 91, 92) but increasing isometrically in both. Depth of byssal notch very variable (text fig. 93) but usually increasing isometrically.

Auricles well demarcated from disc, variable in size, anterior larger than posterior. Posterior auricles meeting hinge line at an obtuse angle and disc at an acute angle. Anterior auricles meeting hinge line at about 90°; that of left valve meeting disc at an acute angle, that of right valve meeting disc at 90° or more. All auricles ornamented with fine comarginal striae and where well preserved, fine divaricate striae.

Height of anterior auricle and length of posterior hinge increasing with approximate isometry (text figs. 94, 95).

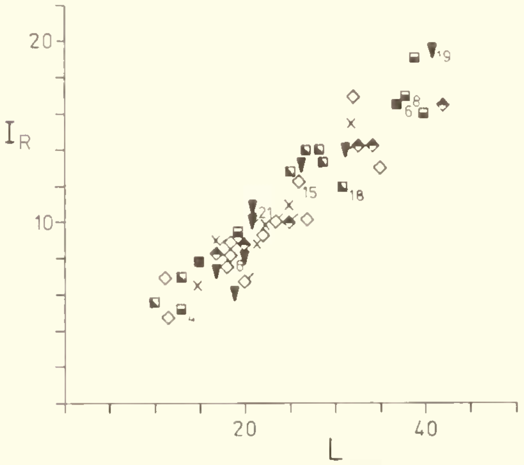


Text fig. 91: *Camptonectes (C.) subulatus* – intersinal distance on left valve/length.

Length of anterior hinge possibly increasing at a decreasing rate (text fig. 96).

Centre of disc exterior smooth in both valves. In well preserved specimens anterior and posterior margins, particularly in the dorsal region, bearing fine divaricate striae (Pl. 4, Fig. 3), rendered 'punctate' by the intersection of comarginal striae. Inner shell layers formed into radial striae of low amplitude (Pl. 4, Fig. 8).

Shell very thin. Outer layer including at least one sub-layer of divaricate fibres.



Text fig. 92: *Camptonectes* (*C.*) *subulatus* – intersinal distance on right valve/length.

4. DISCUSSION

The taxonomy of the weakly ornamented L. Jurassic Pectinidae has been a subject of considerable confusion. Distinction at the generic level is dealt with on pp. 35, 107. The proliferation of names at the specific level has resulted largely from a failure to appreciate the wide but continuous range of variation in metric proportions of the species described in Section 3 and the range of sculptural patterns in the latter resulting from abrasion and dissolution of the thin shell. Four main sculptural patterns (analogous to those observed in *Propeamussium (P.) pumilum* by Holder (1978)) can be recognised in the passage from complete shell preservation to internal mould.

a) Perfect preservation produces shells conforming to the description in Section 3.

b) Loss of the very thin shell layer bearing '*Camptonectes*-ornament' on the lateral disc margins and auricles, leaves a smooth but relatively thick shell bearing traces only of comarginal striae (Pl. 4, Figs. 4, 7).

c) Loss of a further shell layer results in the exposure of radial striae which form a reticulate pattern with the comarginal striae (Pl. 4, Fig. 5; postero-ventral of centre), this standing out as rows of comarginal 'punctae' (cf. a) in suitably fine sediment.

d) Loss of the remainder of the outer layer leaves only the radial striae of the inner shell layers which persist to the internal shell surface and thus appear on moulds (Pl. 4, Fig. 8).

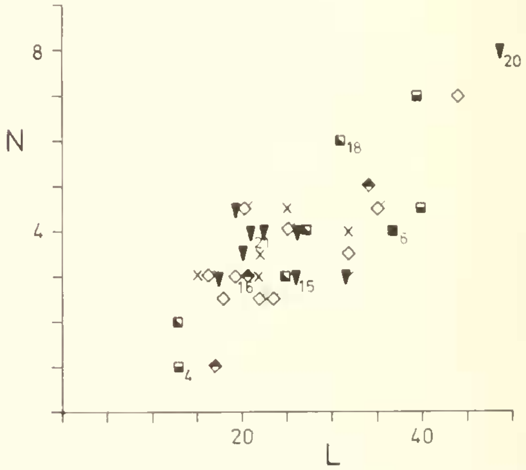
Paired valves often exhibit different sculpture, with the right valve usually representing a more advanced state of abrasion, presumably as the result of more frequent contact with the substratum during life.

BM L40676 (Pl. 4, Fig. 5) exhibits, in different parts of the shell, each of the first three preservation states referred to above, thus convincingly demonstrating that they do not reflect genetic differences. That forms corresponding to preservation state d) are conspecific is made clear by the fact that their metric proportions (specimens marked with a glyph in text figs. 89–96) are inseparable from more perfectly preserved specimens. However, the development of fine radial striae is not restricted to the species under discussion but is also seen in, for instance, small or abraded examples of the 'fine' phenotype of *Chlamys (Ch.) textoria*. Thus, where original material and figures are poor or lacking and descriptions inadequate, there remains considerable taxonomic uncertainty (see below).

Type and original specimens and figures of type specimens apparently corresponding to preservation state a) are: –

1. The holotype (OD) of *Camptonectes mundus* Melville (IGS 28760).
2. The original of *C.* sp. Dechaseaux (NM).
3. The original figure of *C. (C.) fromageti* Hayami.
4. The original figure of '*Pecten*' *lundgreni* Moberg.

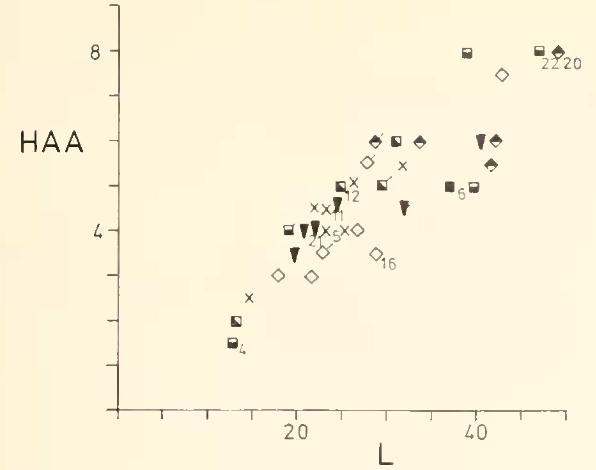
In each of the above cases metric proportions plot within the ranges of text figs. 89–96. Troedsson (1951) referred Moberg's species to *Entolium*. Since he may have had access to the type material it is possible that the appearance of divaricate striae on the original figure may be a misrepresentation of the divaricate fibres which are present in the outer shell layer of *Entolium* as well as the species described in Section 3. In the case of *C. (C.) fromageti* (a species described from Vietnam) it is possible that the lack of '*Camptonectes*-ornament' in the median part of the shell is not due to an original absence but to wear of what was previously a more completely ornamented shell.



Text fig. 93: *Camptonectes* (*C.*) *subulatus* – depth of byssal notch/length.

Type specimens and figures of type specimens corresponding to preservation state b) are: –

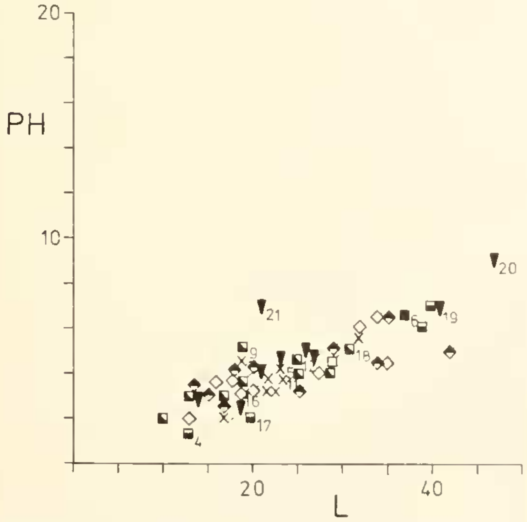
5. A syntype of '*P.*' *calvus* Goldfuss (GPIB 609; Pl. 4, Fig. 4).
6. The two known syntypes of '*P.*' *dehmensis* Ernst (GPIG).



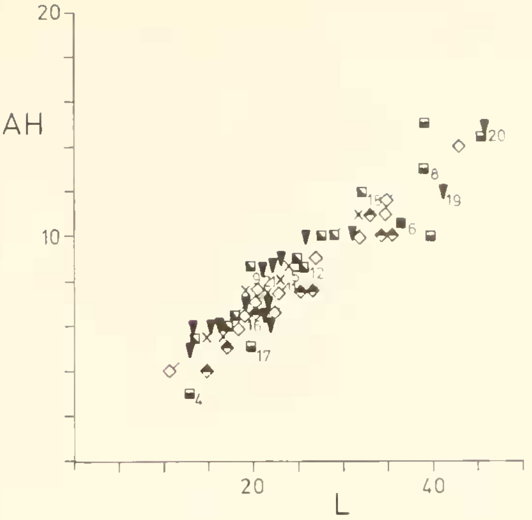
Text fig. 94: *Camptonectes (C.) subulatus* – height of anterior auricle/length.

7. The original figure of *'P.' sublaevigatus* Ernst.
8. The original figure of *'P.' rinki* Lundgren.
9. The original figure of *'P.' (Amusium) Bellampensis* Gemmellaro and Di Blasi.
10. The original figure of *'P.' tingensis* Tilmann.

Numbers 5–9 plot within the ranges of text figs. 89–96. Most of the 16 syntypes of *'P.' tingensis* (GPIB; from Peru) are unlike Tilmann's figure in that they display radial and, in some cases, comarginal ornament. It is therefore very doubtful whether *'P'. tingensis* can be referred to the species described in Section 3. Goldfuss' specific name *calvus* has been applied to figured specimens which by the configuration of the auricles are clearly referable to *Entolium (E.) lunare* (Staesche, 1926; Troedsson, 1951). With the evident possibility of confusion unfigured references to Goldfuss' species in d'Orbigny (1850), Tate and Blake (1876), Joly (1907) and Wobber (1968) cannot safely be synonymised with the species under discussion. Fucini's (1906) figure of Gemmellaro and Di Blasi's species may also refer to *E. (E.) lunare* and Andler's (1858) unillustrated species *'P.' amatus*, described only as a smooth flat shell with comarginal striae, has a similarly equivocal status.



Text fig. 95: *Camptonectes (C.) subulatus* – posterior hinge length/length.



Text fig. 96: *Camptonectes (C.) subulatus* – anterior hinge length/length.

Type specimens and figures and descriptions of type specimens corresponding to preservation state c) are: –

11. The holotype (M) of *'P.' punctatissimus* Quenstedt (GPIT).
12. The original figure of *'P.' Lohbergensis* Emerson.
13. The original description of *'P.' substriatus* Roemer.
14. The single observed type of *'P.' punctatus* Simpson (WM 604).

Metric proportions of 11 and 12 plot within the ranges of text figs. 89–96. Both Quenstedt's and Roemer's specific names have been applied (by respectively Terquem and Piette, 1865 and Staesche, 1926) to quite strongly striate specimens which may be referable to *Chlamys (Ch.) textoria*. Therefore, bearing in mind the remarks made on p. 110 it seems wise to regard inadequately characterised references to these species in Tate and Blake (1876), Cox (1928), Rosenkrantz (1934, 1942), and Dechaseaux (1936) as of uncertain taxonomic position.

Type specimens and figures and descriptions of type specimens corresponding to preservation state d) are: –

15. The sole observed syntype of *'P.' disparilis* Quenstedt (GPIT 4–4–8; Pl. 4, Fig. 6).
16. A syntype of *'P.' strionatis* Quenstedt (GPIT).
17. The holotype (M) of *'P.' Castor* d'Orbigny (MNS).
18. The original figure of *'P.' subulatus* Münster.
19. The original figure of *'P.' jamoignensis* Terquem and Piette.
20. The original figure of *'P.' Tullbergi* Lundgren.
21. The original figure of *'P.' Etheridgii* Tawney.
22. The original figure of *'P.' textilis* Münster.
23. The original description of *'P.' Trigeri* Oppel.

Numbers 15–20 have metric proportions which plot within the ranges of text figs. 89–96. However, *'P.' disparilis* displays particularly prominent radial striae and bearing in mind its horizon of derivation (Planorbis zone) might be an example of *Chlamys (Ch.) valoniensis*. The same may also be the case for *'P.' Etheridgii* (syntypes: IGS 7829, 91801; Pl. 4, Fig. 9) which may also have an anomalously low L/PH (21). N/L of *'P.' textilis* (22) is similarly low and Roemer (1839), who may have examined the syntypes, has applied the name to forms which are reminiscent of *Ch. (Ch.) textoria.* Bearing in mind the remarks made on p. 110 Münster's species can only tentatively be placed in synonymy. The same approach must also be adopted for '*P.*' *Trigeri* (23) which has been applied by Staesche (1926) to specimens whose description recalls that of the 'fine' phenotype of *Ch. (Ch.) textoria.*

In the uncertainty over the affinities of '*P.*' *textilis* the earliest available name for the species described in Section 3 is '*P.*' *subulatus* Münster. The type material appears to be lost thus a neotype may need to be designated. Bearing in mind the remarks made on p. 110 with respect to radially striate specimens, inadequately characterised references to Münster's species in d'Orbigny (1850), Brauns (1871), Moberg (1888), Behmel and Geyer (1966), Berridge and Ivimey-Cook (1967), Wobber (1968) and Hallam (1971) and to Quenstedt's '*P.*' *strionatis* in Jaworski (1916), must be treated with some scepticism. Melville's (1956) '*Ch.*' *subulata securis* is discussed under *Ch. (Ch.) textoria.*

5. STRATIGRAPHIC RANGE

The earliest record of *C. (C.) subulatus* is a single specimen from the pre-Planorbis beds of Gloucestershire (BM L77305). Thereafter the species becomes common in the Planorbis zone (Hettangian) of S. Germany (Staesche, 1926) and in suitable sediments (see Section 8) is thus found in all stages until the U. Pliensbachian. There are no unequivocal records from the L. Toarcian but seven specimens are known from the U. Toarcian of Germany (Ernst, 1923; Staesche, 1926; GPIG). d'Orbigny's (1850) records from the Toarcian of Germany are of doubtful status (see p. 71) but Rosenkrantz (1934) records examples of *C. (C.) subulatus* from the Toarcian of Greenland.

Staesche (1926: 75) records a specimen from the Aalenian whose H/UA (24) and ornamentation is indistinguishable from that of *C. (C.) subulatus.* However, other weakly ornamented Aalenian examples of *C. (Camptonectes)* such as BM L41942 have a higher H/UA (25) and are probably abraded specimens of *C. (C.) auritus.* Thus Staesche's record must be considered questionable in the absence of a figure or a specimen in his collection (GPIT) conforming to the description.

6. GEOGRAPHIC RANGE

Although occurring over a large area of Europe (text fig. 97) *C. (C.) subulatus* is much more common in the northern parts of the region, implying a possible temperature dependance. Staesche (1926) commented on the absence of the species from the Planorbis zone of the Rhone basin, thereby implying a northerly derivation. Except for records from Greenland (see Section 5) there are no certain occurrences of *C. (C.) subulatus* outside Europe (cf. Section 4).

Text fig. 97: *Camptonectes (C.) subulatus* – European distribution.

7. DESCRIPTION OF ECOLOGY

In the Hettangian *C. (C.) subulatus* occurs in sandstones in E. France (Terquem and Piette, 1865; fauna p. 87). Calcarenites are the site of probable occurrences of the species in the Planorbis zone of S. Wales (Wobber, 1968). In S. Germany marly limestones of the same age contain common examples of *C. (C.) subulatus* (Staesche, 1926) reaching a maximum height of 32 mm (GPIT). The species is also common in oolitic limestones of the Angulata zone and L. Sinemurian in the same area. In the latter substage it attains a maximum height of 30.5 mm (GPIT) and is associated with *Entolium (E.) lunare.*

In the U. Sinemurian *C. (C.) subulatus* occurs in the Obtusum zone chamosite oolites of the Frodingham Ironstone (fauna p. 69) but it is greatly outnumbered by *E. (E.) lunare.* In the Raricostatum zone of Yorkshire *C. (C.) subulatus* occurs commonly in silty shales in association with *Pseudopecten (Ps.) equivalvis, Pseudolimea, Antiquilima, Pinna, Gryphaea, Pleuromya, Procerithium, Tetrarhynchia* and belemnites (Sellwood, 1972). *E. (E.) lunare* is quite rare. Numbers of *C. (C.) subulatus* are particularly high in the vicinity of large *Pinna*. A similar association characterises the Jamesoni zone (L. Pliensbachian) of Yorkshire and the U. Sinemurian/L. Pliensbachian sequence in S. Germany where *C. (C.) subulatus* reaches a maximum height of 37.5 mm (GPIT). In sediments of the same age but with a somewhat restricted benthos (mainly consisting of protobranchs, *Inoceramus* and *Oxytoma* [Sellwood, 1972]) in Dorset, *C. (C.) subulatus* is rare.

C. (C.) subulatus occurs commonly in shales of the Margaritatus zone (U. Pliensbachian) in Yorkshire where *E. (E.) lunare* is rare. However the latter species is common and *C. (C.) subulatus* is rare in U. Pliensbachian sandstones and ironstones. The maximum height attained by *C. (C.) subulatus* in the substage is 42 mm (GPIT).

Sparse records from the U. Toarcian of Germany (see Section 5) are from grey marlstones containing a somewhat restricted benthic fauna in which *C. (C.) subulatus* attains a maximum height of 52.5 mm (Staesche, 1926).

The species is unknown in the low salinity marginal marine deposits of the Hettangian in N. W. Germany (Huckriede, 1967) and W. Portugal (Böhm, 1901) and does not appear until the Raricostatum zone (U. Sinemurian) in the transgressive sequence of the Lossiemouth borehole (Berridge and Ivimey-Cook, 1967). However, Lundgren (1881) records the species from paralic cyclic sediments in the Hettangian of Scania although it is not clear whether the species occurs in anything but the most fully marine beds. *C. (C.) subulatus* is not recorded commonly in the area until the L. Sinemurian when conditions were continuously marine (Troedsson, 1951).

C. (C.) subulatus is not known to occur commonly other than in the examples discussed above. However, isolated specimens are widely recorded (text fig. 97).

8. INTERPRETATION OF ECOLOGY

Apart from an apparent abhorrence of the soupy substrates and low oxygen tension associated with bituminous shale deposition (indicated by the absence of the species from the L. Toarcian of Europe) *C. (C.) subulatus* seems to have been a eurytopic species with respect to substrate. However, abundance data indicates a definite preference for argillaceous substrates at least after the L. Sinemurian. Since this is essentially the reverse of the pattern exhibited by *Entolium (E.) lunare* it is possible that such niche differentiation was caused by competition, perhaps for juvenile attachment sites, between earlier, more eurotypic representatives of the species.

There is little evidence to suggest that *C. (C.) subulatus* could tolerate the high stress environments associated with low or fluctuating salinity. The scarcity of the species in sediments where the faunal diversity is only somewhat reduced suggests that *C. (C.) subulatus* could only thrive in the most stable environments. However, in these cases the absence of *Pinna*, which by its frequent association with *C. (C.) subulatus* may have served as a byssal attachment site (see Section 9), could be the cause of the scarcity of the species rather than any intolerance of slightly increased stress.

A Recent morphological analogue of *C. (C.) subulatus*, '*Pecten*' *alcocki* Smith, lives byssally attached to siliceous sponges in the bathyal zone (Knudsen, 1972).

9. FUNCTIONAL MORPHOLOGY

The thin shell, low convexity and minimal ornamentation of all examples of *C. (C.) subulatus* and the marked byssal notch and small adult size of most, are paradigmatic for a byssally suspended mode of life (tightly fixed).

It is not clear at what size, if any, the Recent analogue '*P.*' *alcocki* loses the ability to attach by a byssus. However, late populations of *C. (C.) subulatus*, reaching a maximum height of over 50 mm, must be near the upper limit for this mode of life and may have been forced to recline in the later stages of ontogeny.

Ontogenetic increase in umbonal angle probably facilitated escape from predators by swimming at even the largest sizes. In spite of the juxtaposition of radial and divaricate elements in the shell, strength and stiffness must have been very low, thus it is extremely doubtful whether *C. (C.) subulatus* could have resisted attempted predation by means of a 'siege' policy.

10. ORIGINS AND EVOLUTION

Staesche (1926) considered that forms referable to *C. (C.) subulatus* were derived from *Chlamys trigeri* (a possible synonym, see Section 4) in the Planorbis zone. He believed the latter species to be synonymous with '*Pecten*' *simplex* Winkler (1861), a species from the Kössen Beds (U. Trias) of Bavaria. However, '*P.*' *simplex* has strong radial ornament and is unlikely to have close affinities with *C. (C.) subulatus*. A more likely ancestor for the latter is '*Pleuronectites*' *laevigatus* Schlotheim, a smooth species, common in the M. Trias.

There appear to be no morphological trends in *C. (C.) subulatus* apart from a general increase in maximum height from 32 mm (Hettangian) to 30.5 mm (L. Sinemurian) to 37.5 mm (L. Pliensbachian) to 42 mm (U. Pliensbachian) to 52.5 mm (U. Toarcian). This, together with a narrowing of the range of favourable substrates, probably indicates the prevalence of 'K' selection (Gould, 1977).

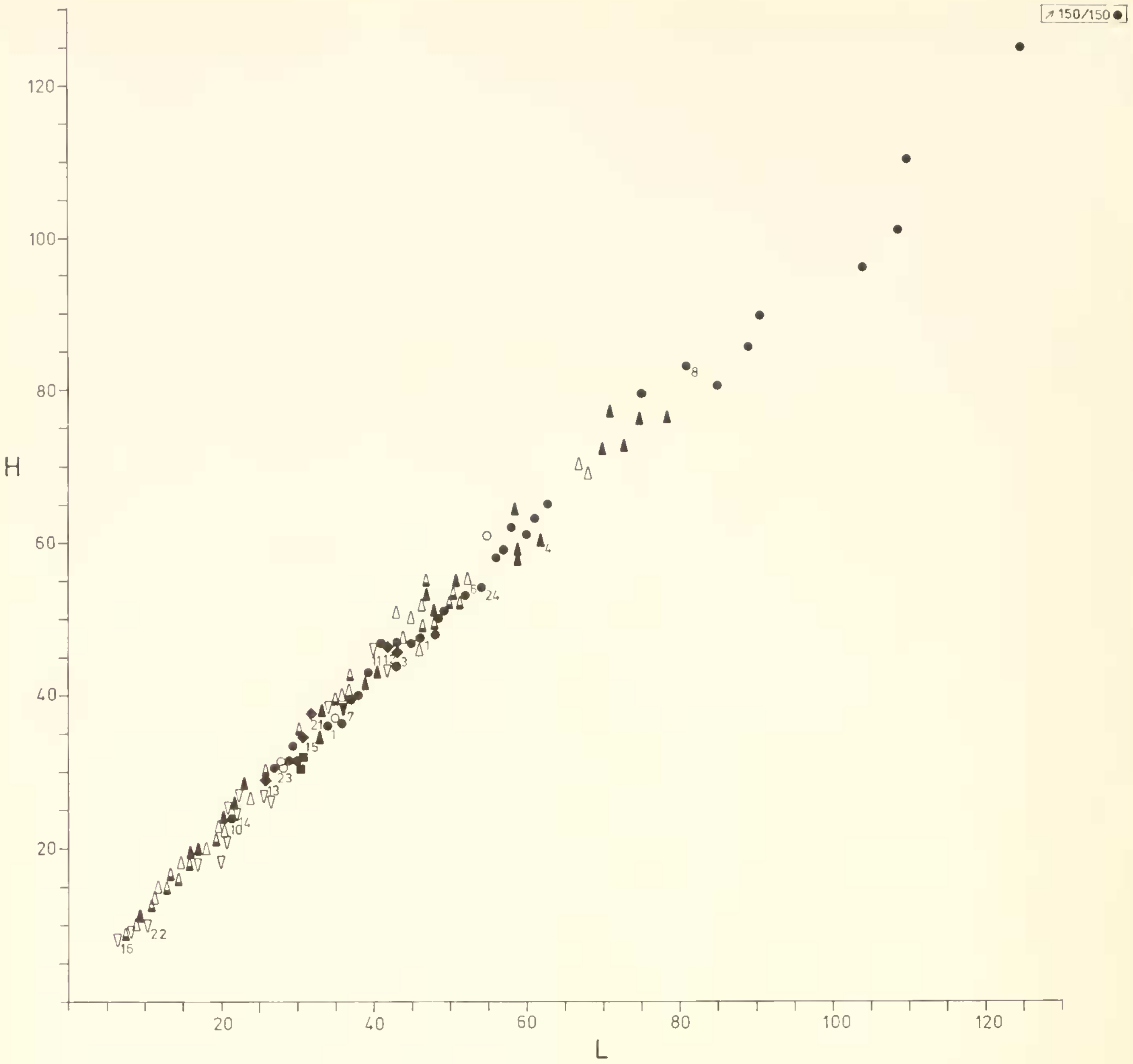
The post U. Toarcian extinction of *C. (C.) subulatus* may have been caused by the widespread development of shallow water facies over N. Europe, producing unfavourable conditions for late representatives of the species.

Camptonectes (Camptonectes) auritus (Schlotheim 1813)

Pl. 3, Figs. 25–40; text figs. 98–107

Synonymy

1676	*Pectinites*; Plot, p. 104, pl. 4, fig. 11.
1678	*Pectinites*; Lister, pl. 9, fig. 51.
1813	*Chamites auritus* sp. nov; Schlotheim, p. 103.
v* 1818	*Pecten lens* sp. nov; J. Sowerby, p. 3, pl. 205, figs. 2, 3.
v* 1818	*Pecten arcuata* sp. nov; J. Sowerby, p. 4, pl. 205, figs. 5, 7.
1822	*Pecten Maltonensis* sp. nov; Young and Bird, p. 235, pl. 9, fig. 1.



Text fig. 98: *Camptonectes (C.) auritus* – height/length.

v* 1833 *Pecten comatus* sp. nov; MÜNSTER in GOLDFUSS, p. 50, pl. 91, figs. 5a, 5b.

1939 *Pecten Buchi* sp. nov; ROEMER, p. 27, pl. 13, figs. 8a, 8b.

1939 *Pecten lens* J. SOWERBY; ROEMER, p. 27.

1839 *Pecten Dechem* sp. nov; ROEMER, p. 28, pl. 18, fig. 25.

1839 *Pecten arcuatus* J. SOWERBY; BEAN, p. 60.

1839 *Pecten lens* J. SOWERBY; BEAN, p. 60.

? 1843 *Pecten lens* J. SOWERBY; QUENSTEDT, p. 337.

1850 *Pecten Lusitanicus* sp. nov; SHARPE, p. 189, pl. 24, fig. 3.

1850 *Pecten Saturnus* sp. nov; D'ORBIGNY, v. 1, p. 284 (BOULE, 1910, v. 5, p. 69).

v 1850 *Pecten Midas* sp. nov; D'ORBIGNY, v. 2, p. 54 (BOULE, 1932, v. 21, p. 12, pl. 2, figs. 3–6).

non 1853 *Pecten lens* J. SOWERBY; MORRIS and LYCETT, p. 11, pl. 2, fig. 1.

non 1853 *Pecten arcuatus* J. SOWERBY; MORRIS and LYCETT, p. 11, pl. 1, fig. 18.

1853 *Pecten Saturnus* D'ORBIGNY; CHAPUIS and DEWALQUE, p. 215, pl. 29, fig. 4.

v 1858 *Pecten lens* J. SOWERBY; QUENSTEDT, p. 322, pl. 44, fig. 12, p. 354, pl. 46, fig. 20, pl. 48, fig. 8, p. 432, pl. 59, fig. 4 (non pl. 59, fig. 3).

1860 *Pecten lens* J. SOWERBY; COQUAND, p. 70.

? 1862 *Pecten Delessei* sp. nov; ÉTALLON in THURMANN and ÉTALLON, p. 266, pl. 37, fig. 6.

1862 *Pecten Parandieri* sp. nov; ÉTALLON in THURMANN and ÉTALLON, p. 266, pl. 37, fig. 6.

non 1863 *Pecten Midas* D'ORBIGNY, DOLLFUS, p. 79, pl. 14, figs. 1–3.

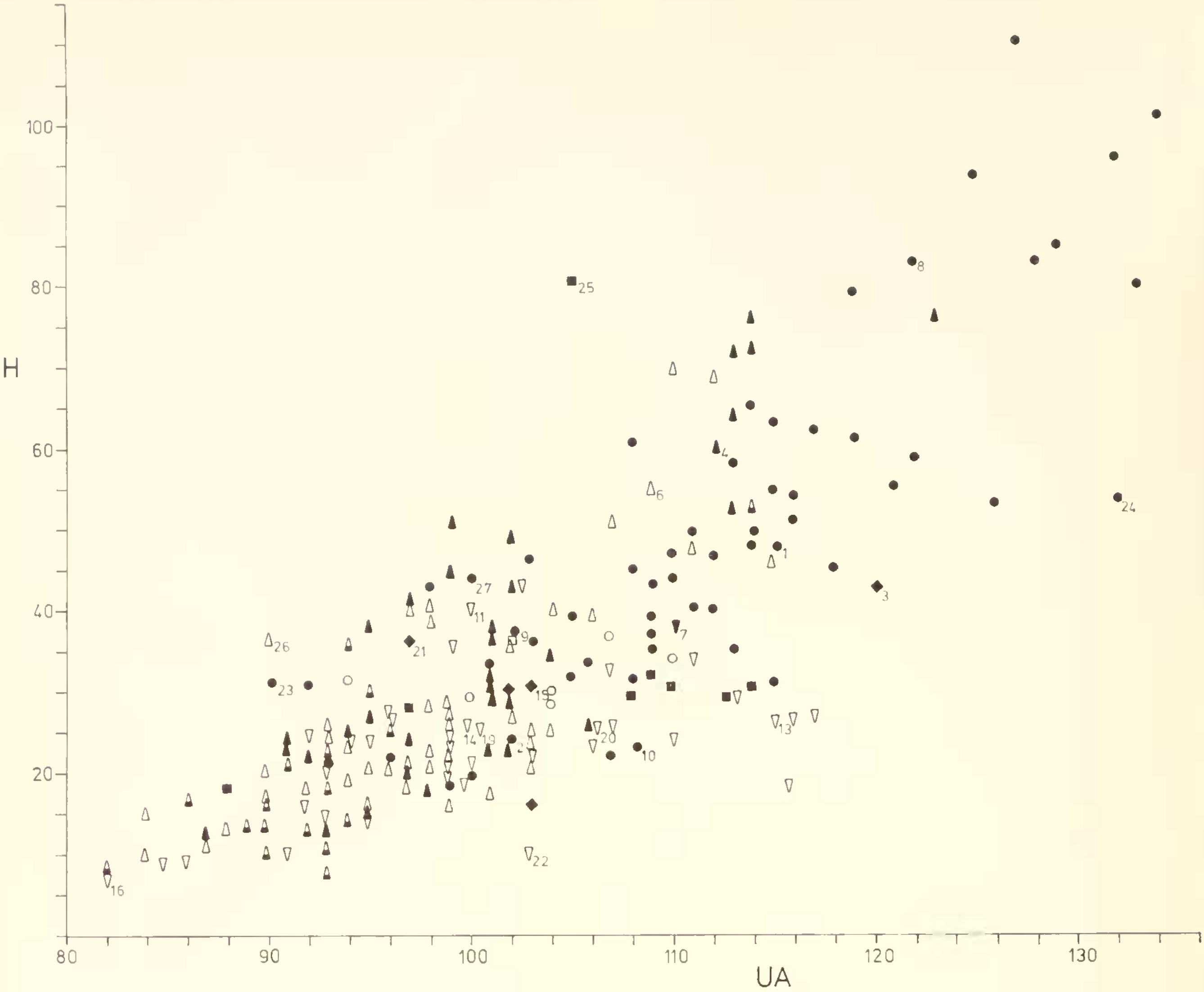
1864 *Pecten lens* J. SOWERBY; V. SEEBACH, p. 99.

1864 *Pecten comatus* MÜNSTER; V. SEEBACH, p. 99.

1866 *Pecten morini* sp. nov; DE LORIOL in DE LORIOL and PELLAT, p. 107, pl. 10, fig. 6.

? 1866 *Pecten validus* sp. nov; Lindstrom, p. 15, pl. 3, figs. 5, 6.
1867 *Pecten lens* J. Sowerby; Laube, p. 12.
v* 1867 *Pecten aratus* sp. nov; Waagen, p. 630, pl. 31, fig. 3.
? 1869 *Pecten lens* J. Sowerby; Terquem and Jourdy, p. 128.
1871 *Pecten Nitescens* sp. nov; Phillips, p. 330, pl. 15, fig. 2.
? 1872 *Pecten Midas* d'Orbigny; de Loriol et al., p. 389, pl. 22, figs. 12, 13.
? 1874 *Pecten subvitreus* sp. nov; Gemmellaro and Di Blasi, p. 122, pl. 3, figs. 11, 12.
? 1875 *Pecten midas* d'Orbigny; de Loriol and Pellat, p. 193.
1875 *Pecten Etalloni* sp. nov; de Loriol in de Loriol and Pellat, p. 197, pl. 22, figs. 8, 9.
1879 *Pecten lens* J. Sowerby; Branco, p. 110.
non 1880 *Pecten midas* d'Orbigny; Damon, pl. 17, fig. 4.
v* 1880 *Pecten Clypeatus* sp. nov; Witchell, p. 131, pl. 5, figs. 1a, 1b.
1882 *Pecten gracilis* sp. nov; Alth, p. 294, pl. 21, figs. 15, 16.
? 1883 *Pecten lens* J. Sowerby; Lahusen, p. 23, pl. 2, figs. 1, 2.
v* 1883 *Pecten triformis* sp. nov; Whidborne, p. 502, pl. 16, fig. 3.
1886b *Pecten Neumayri* sp. nov; De Gregorio, p. 15, pl. 2, figs. 5, 6.
1886c *Pecten anughus* sp. nov; De Gregorio, p. 10, pl.4, figs. 12a–c.
? 1888 *Pecten lens* J. Sowerby; Schlippe, p. 128.
1890 *Pecten lens* J. Sowerby; Tausch, p. 13, pl. 7, fig. 9.
1893 *Pecten Nais* sp. nov; de Loriol, p. 310, pl. 33, figs. 3, 4.
1893 *Pecten Letteroni* sp. nov; de Loriol in de Loriol and Lambert, p. 140, pl. 10, fig. 8.
non 1894 *Pecten Buchi* Roemer; de Loriol, p. 53, pl. 6, fig. 7.
? 1896 *Pecten* cf. *lens* J. Sowerby; Semenow, p. 64.
? 1898 *Pecten lens* J. Sowerby; Greppin, p. 129.
? 1900 *Chlamys lens* (J. Sowerby); Cossmann, p. 170.
? *1905* *Pecten (Camptonectes) arcuatus* J. Sowerby; Kilian and Guébhard, p. 758.
? *1905* *Pecten (Camptonectes) lens* J. Sowerby; Kilian and Guébhard, p. 758.
? *1907* *Pecten lens* J. Sowerby; Deninger, p. 454.
1910 *Camptonectes lens* (J. Sowerby); Lissajous, p. 363, pl. 10, fig. 6.
1915 *Pecten lens* J. Sowerby; Krenkel, p. 296.
v* 1916 *Camptonectes aalensis* sp. nov; Paris and Richardson, p. 523, pl. 14, figs. 3a, 3b.
1917 *Pecten lens* J. Sowerby; Borissiak and Ivanoff, p. 19, pl. 1, figs. 3, 6, 7, 9, 11.
p 1923 *Camptonectes lens* (J. Sowerby); Lissajous, p. 165.
? 1924 *Camptonectes* cf. *bellistriatus* (Meek); McLearn, p. 47, pl. 5, figs. 4, 5.
? 1924 *Camptonectes* sp; McLearn, p. 47, pl. 5, fig. 6.
1925 *Pecten lens* J. Sowerby; Read et al., p. 80.
1925 *Pecten (Camptonectes) lens* J. Sowerby; Dubar, p. 285.
? *1926* *Camptonectes lens* (J. Sowerby); Roman, p. 175.
v* 1926 *Camptonectes psilonoti* sp. nov; Staesche, p. 74, pl. 3, fig. 2.
pv 1926 *Camptonectes lens* (J. Sowerby); Staesche, p. 76, pl. 2, fig. 8.
v non 1926 *Camptonectes lens* var. *annulatus* (J. de C. Sowerby); Staesche, p. 79, pl. 3, fig. 12.
v* 1926 *Camptonectes giganteus* sp. nov; Arkell, p. 544, pl. 33, fig. 1.
v 1930a *Camptonectes lens* (J. Sowerby); Arkell, p. 94, pl. 7, fig. 1, (1931a) pl. 9, figs. 4–7.
v* 1930a *Camptonectes sandsfootensis* sp. nov; Arkell, p. 101, pl. 8, fig. 3.
pv non 1931a *Chlamys (Aequipecten) midas* (d'Orbigny); Arkell, p. 115, pl. 11, figs. 17–21.
? 1931 *Pecten (Camptonectes)* cf. *lens* J. Sowerby; Sokolov and Bodylevsky, p. 55, pl. 4, fig. 7.
1931 *Pecten (Aequipecten) validus* Lindstrom; Sokolov and Bodylevsky, pp. 58, 59, pl. 3, figs. 1, 2.
p 1934 *Pecten (Camptonectes) lens* J. Sowerby; Stoll, p. 22.
non 1934 *Pecten (Camptonectes) lens* var. *annulatus* J. de C. Sowerby; Stoll, p. 22.
1935 *Pecten (Camptonectes)* aff. *lens* J. Sowerby; Spath, p. 56.
v 1936 *Camptonectes lens* (J. Sowerby); Dechaseaux, p. 30, pl. 4, figs. 11, 14 (non figs. 9, 9a).
non 1936 *Camptonectes lens* var. *exaratus* (Terquem and Jourdy); Dechaseaux, p. 30.
1936 *Camptonectes Mairei* sp. nov; Dechaseaux, p. 37, pl. 5, figs. 8–10.
? 1936 *Camptonectes aalensis* Paris and Richardson; Wandel, p. 480.
1936 *Camptonectes morini* (de Loriol); Spath, p. 105, pl. 41, figs. 5, 6.
1936 *Camptonectes suprajurensis* (Buvignier); Spath, p. 106, pl. 41, figs. 2–4, pl. 42, fig. 9, pl. 43, fig. 4 (?Buvignier sp.).
1939 *Camptonectes lens* (J. Sowerby); Stefanini, p. 173, pl. 99, fig. 12.
non 1941 *Pecten (Camptonectes) lens* J. Sowerby; Leanza, p. 173, pl. 10, figs. 1, 2.
? 1951 *Chlamys interpunctata* sp. nov; Troedsson, p. 214, pl. 20, fig. 18.
1952 *Camptonectes auritus* (Schlotheim); Cox, p. 23, pl. 2, fig. 6.
1952 *Camptonectes lens* (J. Sowerby); Makowski, p. 17.
? 1953 *Camptonectes grandis* (Hector); Marwick, p. 100, pl. 4, figs. 6, 7.
1953 *Camptonectes giganteus* Arkell; Donovan, p. 70, pl. 15, fig. 1.
? *1957* *Camptonectes bellistriatus* (Meek); Frebold, p. 21
1961 *Camptonectes* cf. *auritus* (Schlotheim); Hayami, p. 319.
v 1963 *Camptonectes* sp; Kirkaldy, p. 129.
? 1964 *Camptonectes stygius* (White); Imlay, p. 25, pl. 2, figs. 1–10.
1965 *Camptonectes auritus* (Schlotheim); Cox, p. 54.
? *1966* *Camptonectes lens* (J. Sowerby); Behmel and Geyer, p. 28.
? *1974* *Camptonectes bellistriatus* (Meek); R. Wright, pp. 428, 430.
1974 *Camptonectes greenhoughi* sp. nov; Skwarko, p. 80, pl. 26, figs. 11, 13–17.
1975 *Camptonectes sandsfootensis* Arkell; Sykes, p. 217.
1975 *Camptonectes giganteus* Arkell; Sykes, p. 218.
1977 *Camptonectes (Camptonectes) morini* (de Loriol); Kelly, p. 77, pl. 5, figs. 1–5, 7–9.
v 1978 *Camptonectes (Camptonectes) auritus* (Schlotheim); Duff, p. 66, pl. 5, figs. 22, 25, text. fig. 22.

Neotype of *Chamites auritus* Schlotheim 1813, p. 103 designated by Duff, 1978, p. 66; BM L80525; figured Duff, 1978, pl. 5, fig. 25; Pl. 3, Fig. 25 herein; Shell-cum-Pebble Bed (Oxfordian), Headington, Oxford.



Text fig. 99: *Camptonectes (C.) auritus* – height/umbonal angle.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

None given; reference to Lister (1678, pl. 9, fig. 15).

2. DIAGNOSIS

Distinguished from *C. (C.) lamınatus* by the generally finer ornament, from *C. (C.) subulatus* by the presence of ornament on all parts of the disc and from *C. (C.) virdunensis* by the more orbicular disc.

3. DESCRIPTION

Disc sub-ovate, higher than long early in ontogeny, growing allometrically to become sub-orbicular and finally sub-ovate, longer than high (text fig. 98), near the maximum height of 150 mm (OUM J2361). Umbonal angle very variable (text fig. 99), increasing at a decreasing rate during ontogeny. Dorsal margins concave, disc flanks low.

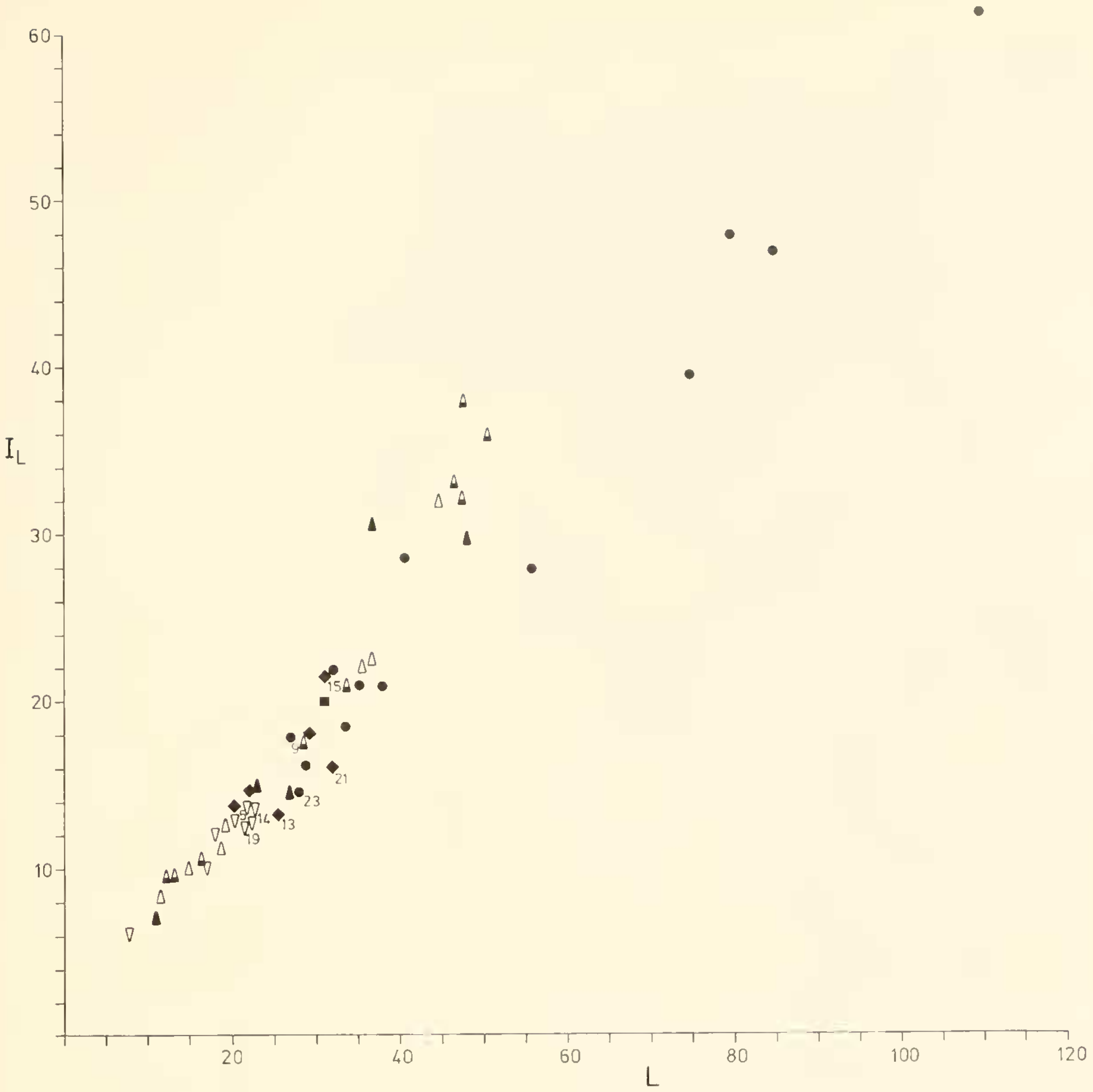
Inequilateral, anterior greater than posterior half length; inequivalve, low convexity, left valve more convex than right. Intersinal distance variable, greater in left valve than right, apparently increasing with respect to length at a slower rate in U. Jurassic cf. M. Jurassic representatives (text figs. 100, 101). Byssal notch depth variable, moderate to large (text fig. 102), increasing isometrically.

Auricles well demarcated from disc, variable in size, anterior larger than posterior. Anterior auricle of right valve meeting hinge line and disc at about 90°. Other auricles meeting hinge line at an obtuse angle and disc at an acute angle. All auricles ornamented with fine comarginal striae. Posterior auricle of right valve also bearing divaricate striae.

Height of anterior auricle and length of anterior hinge variable, increasing with respect to length at a decreasing rate in all populations (text figs. 103, 104). Length of posterior hinge variable, increasing with respect to length at a slower rate in U. cf. M. Jurassic representatives (text fig. 105).

Disc exterior ornamented with a variable number of fine divaricate striae (e. g. Pl. 3, Figs. 32, 33) increasing in number by intercalation and rendered 'punctate' by the intersection of growth lines.

Shell thickness low to moderate.



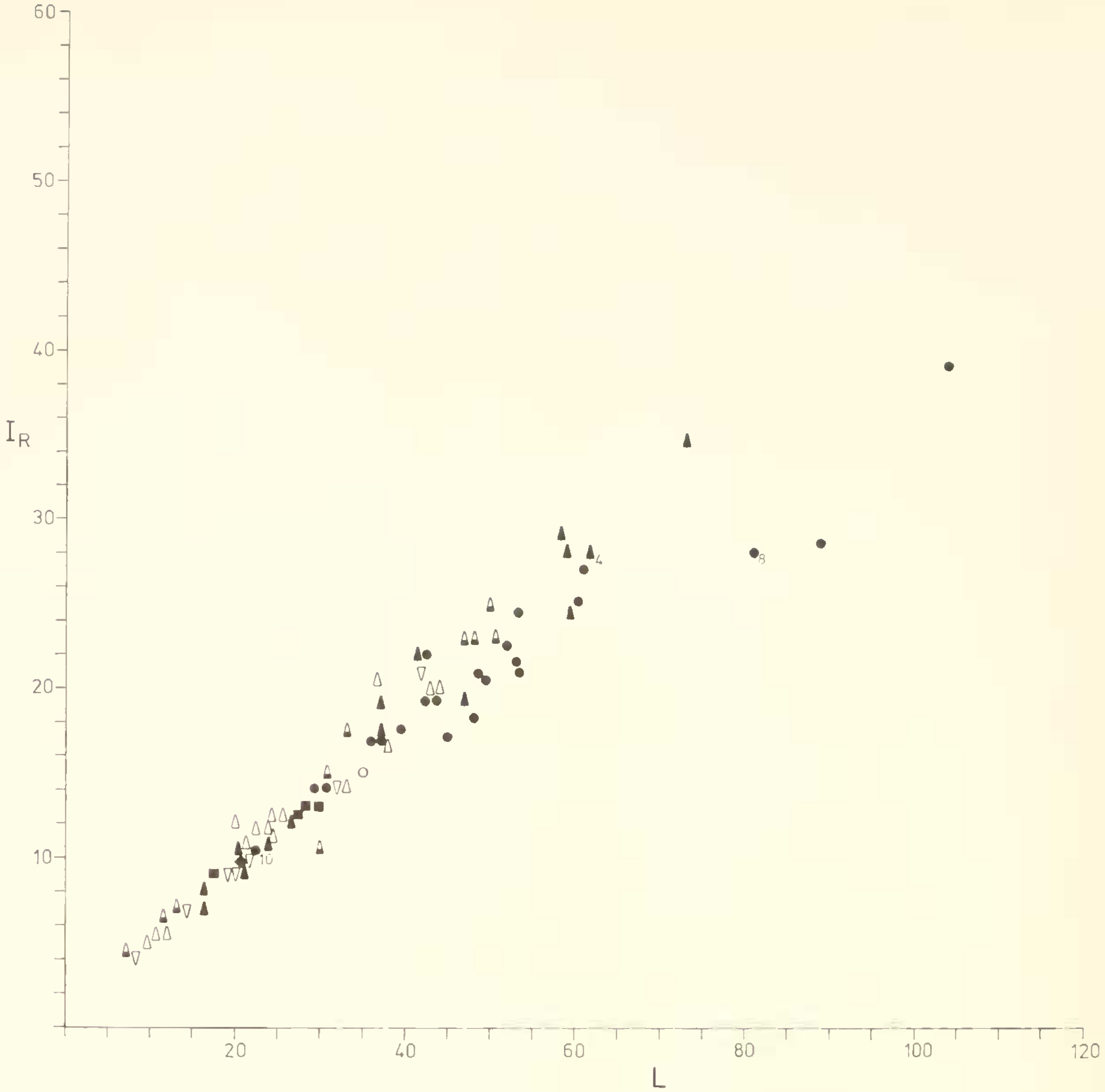
Text fig. 100: *Camptonectes (C.) auritus* – intersinal distance on left valve/length.

4. DISCUSSION

The systematics of the essentially finely-ornamented and orbicular species of *C. (Camptonectes)* described above has been the subject of much, often heated, debate. Failure to appreciate the range of static, ontogenetic and ecophenotypic variation in both ornamentation and metric proportions, allied to the typological approach of early authors has led to the designation of a plethora of specific names. The indiscriminate lumping of many of these names by early revisionists who failed to examine type material has led to a secondary source of confusion (see ARKELL, 1930a for a review). However, later revisionists have also been lamentably at fault in their failure to unite stratigraphically separated but morphologically indistinguishable forms. The result is almost unparalleled nomenclatural chaos.

Minor differences in metric proportions of early and later populations (see Section 3) of individuals whose ornament is within the range defined by Pl. 3, Figs. 32, 33, can be explained as the result of phyletic neoteny (see section 10), since there is no evidence for the existence of separate lineages. Similarly the availability of an explanation in terms of stunting (see Sections 8, 10) does not favour the recognition of certain localised populations, typified by a low H/UA ratio, as separate species. 'Ecophenotypic' rather than 'genetic' variation can also be held to account for the existence of specimens with relatively strong comarginal ornament (Pl. 3, Fig. 31) and specimens with the median sector of the shell unornamented (Pl. 3, Fig. 38). The former is probably the result of some environmental disturbance (as might be caused by tides, storms or attempted predation) interrupting the normal pattern of growth (CLARK, 1974) while the latter is almost certainly the result of abrasion since it is confined to those parts of the shell which have been exposed to the environment for the longest period. Moreover in paired valves it is invariably the right valve (which was almost certainly in contact with the substrate and therefore subject to the most abrasion) which exhibits reduced ornamentation.

The framework of variation erected above is the basis for the following taxonomic discussion.



Text fig. 101: *Camptonectes (C.) auritus* – intersinal distance on right valve/length.

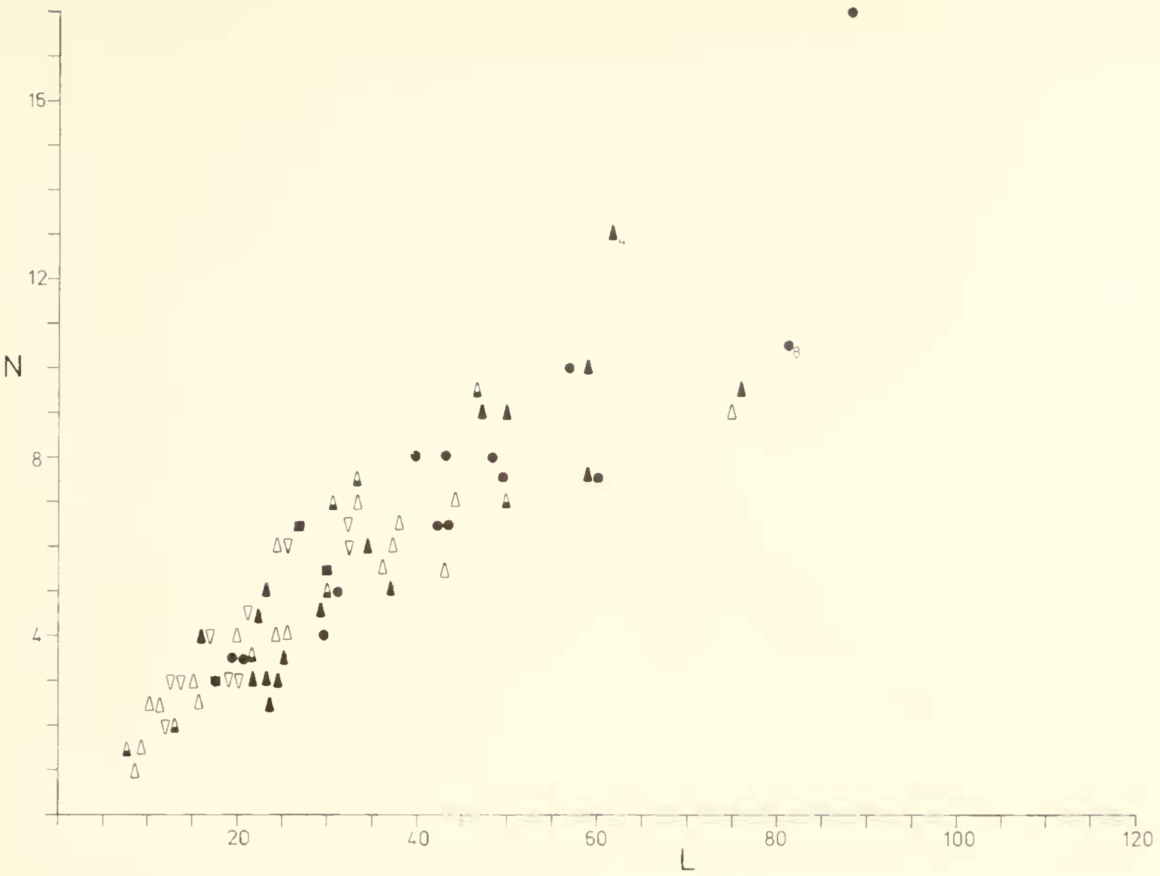
Type specimens which are inseparable from the species described in Section 3 by metric criteria are: –

1. The syntypes of *'Pecten' lens* J. Sowerby (BM L80525, 43326; Pl. 3 Fig. 25).
2. A syntype of *'P.' arcuata* J. Sowerby (BM L80528; Pl. 3, Fig. 30).
3. The sole observed type of *'P.' comatus* Münster (BSPHG AS VII 634; Pl. 3, Fig. 27).
4. The sole observed syntype of *'P.' aratus* Waagen (BSPHG AS XXII 32; Pl. 3, Fig. 34).
5. The sole observed type of *'P.' Letteroni* de Loriol (MNS B03988; Pl. 3, Fig. 28).
6. The sole observed syntype of *Camptonectes aalensis* Paris and Richardson (BM L41942; Pl. 3, Fig. 40).
7. The holotype (M) of *C. Psilonoti* Staesche (GPIT).
8. A syntype of *C. giganteus* Arkell (OUM J2359).

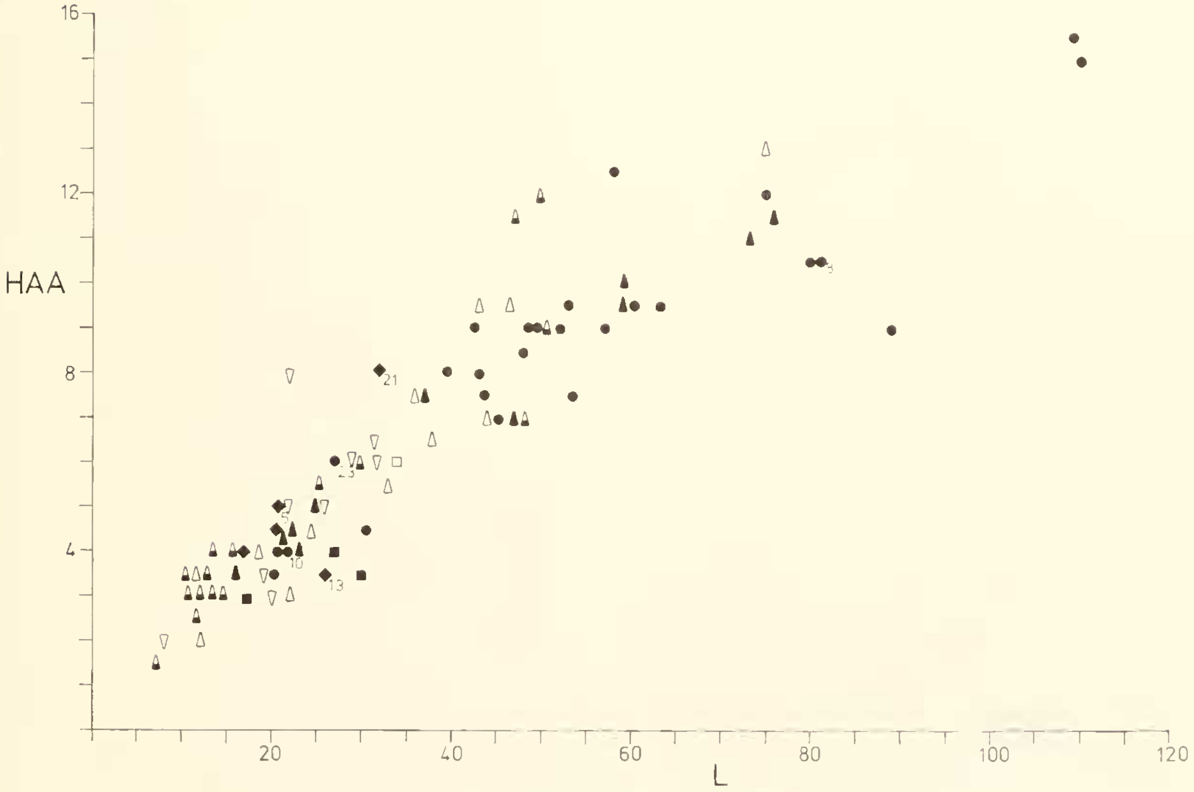
Figures of type and original specimens indistinguishable by metric criteria from the species described in Section 3 are those of: –

9. *Pectinites* Plot.
10. *'P.' Decheni* Roemer.
11. *'P.' Lusitanicus* Sharpe.
12. *'P.' Midas* d'Orbigny (Boule, 1932).
13. *'P.' Parandieri* Étallon.
14. *'P.' morini* de Loriol.
15. *'P.' Etalloni* de Loriol.
16. *'P.' gracilis* Alth.
17. *'P.' Nais* de Loriol.
18. *C. sandsfootensis* Arkell (paratypes: OUM J2360, J2361).
19. *C. Mairei* Dechaseaux.
20. *C. suprajurensis* (Buvignier); Spath (see p. 131 for a discussion of Buvignier's species).

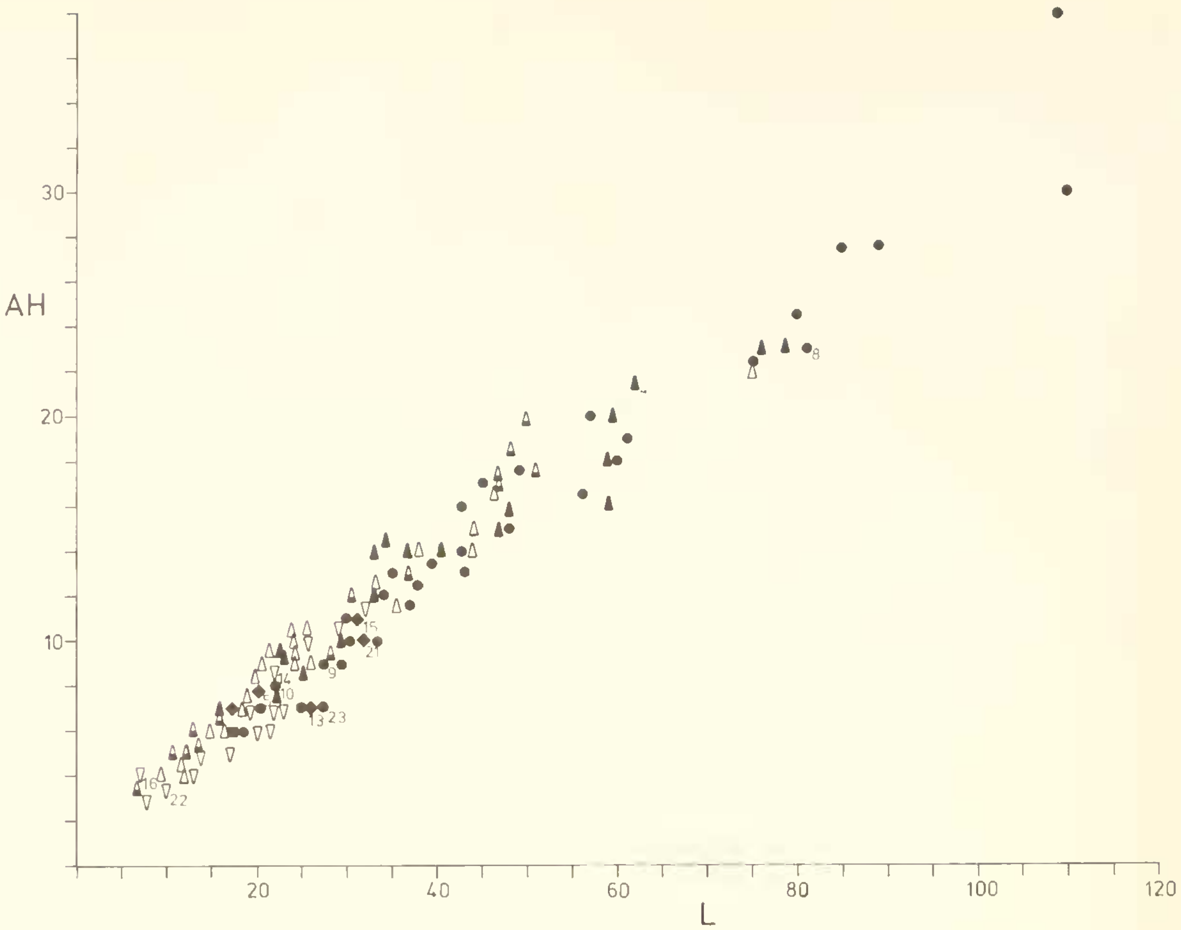
Of the above species, numbers 4, 6, 7, 8, 9, 13, 16 and 18 refer to specimens which are unornamented in the median sector of the shell while 19 refers to a specimen with strong comarginal ornament, both of which characteristics are considered to be features of 'ecophenotypic' variation (see above).



Text fig. 102: *Camptonectes (C.) auritus* – depth of byssal notch/length.



Text fig. 103: *Camptonectes (C.) auritus* – height of anterior auricle/length.



Text fig. 104: *Camptonectes (C.) auritus* – anterior hinge length/length.

The remaining measured species exhibit the typical ornament of the species described in Section 3. Arkell (1926) considered that large size (H: ≃ 125) was sufficient ground for erecting *C. giganteus* (8) but the presence of intermediate sized specimens (text fig. 98) belies this reasoning. The abnormally high H/UA ratio considered by Arkell (1930a) to be distinctive of *C. sandsfootensis* is merely the result of incorrect measurement. The original figure yields a value (H: 123, UA: ≃ 145) well within the range of text fig. 99 projected to larger sizes.

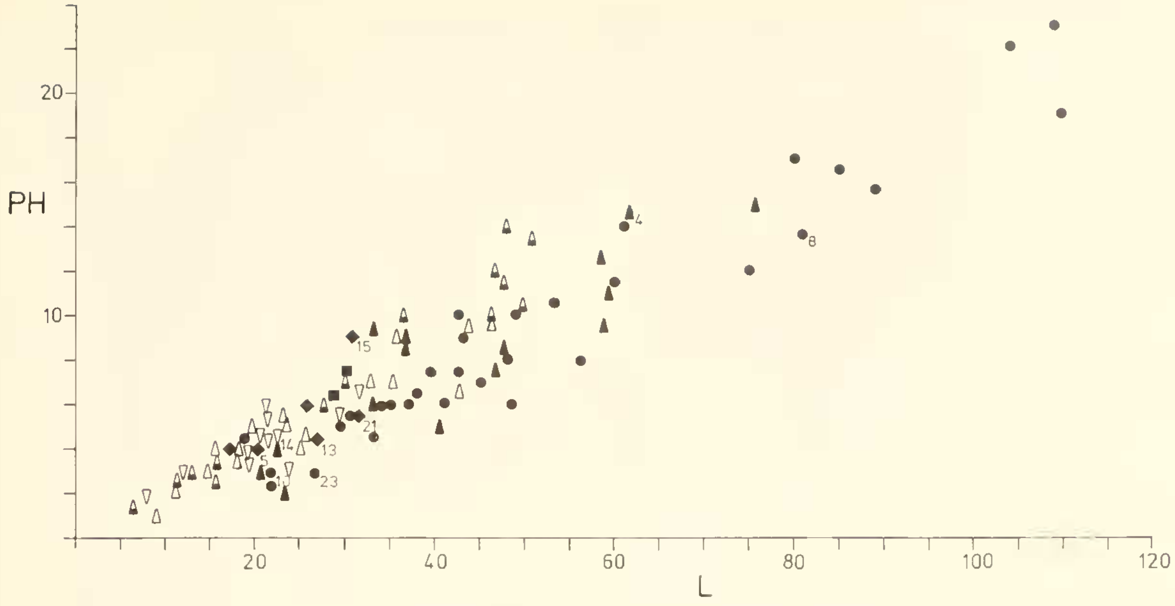
The original figure of '*P.*' *Delessei* Étallon (21) is inseparable from the species described in Section 3 by L/AH, L/PH, L/I_L and L/HAA but the anomalously high H/L and H/UA suggest that it may be equivalent to *C. (C.) suprajurensis*. '*P.*' *subvitreus* Gemmellaro and Di Blasi (22) has an anomalously low H/UA but this could well be due to imprecise measurement by the authors of the species. H/L and L/AH of the original figure is inseparable from the species described in Section 3. The figure of '*P.*' *Buchi* Roemer apprently depicts a left valve which has been reversed through the process of printing from a copper engraving. Further inaccuracies in reproduction may account for the seemingly high H/UA and L/AH (23) of a specimen whose ornament and other metric proportions are indistinguishable from the species described in Section 3.

Species for which types and figures are either unavailable or of insufficient quality for measurement are considered below.

C. cf. *bellistriatus* (Meek); McLearn and *C.* sp; McLearn from N. America have ornament which is within the range defined by Pl. 3, Figs. 32, 33. However, a specimen referred to the former species (BM L58934) from the Oxfordian of Wyoming has an exceptionally low H/UA (24) thus it may be that finely ornamented N. American *C. (Camptonectes)* are specifically distinct. *C. grandis* (Hector); Marwick from N. Zealand is indistinguishable on the basis of ornament but is reported to have only a small byssal notch. Although the size of the latter is variable in the species described in Section 3 it seems unwise at present to synonymise the species.

'*P.*' *triformis* Whidborne (holotype BM L73166; Pl. 3, Fig. 35), '*P.*' *nitescens* Phillips and *C. stygius* (White); Imlay are characterised by a lack of ornament in the median shell sector, which may be considered an aspect of 'ecophenotypic' variation (see above). *C. stygius* is however derived from N. America and therefore cannot be certainly synonymised with the species described in Section 3 (see above).

Boule (1910) considered the single type of '*P.*' *Saturnus* d'Orbigny in the MNO to be specifically indeterminate and created a neotype from the specimen figured in Chapuis and Dewalque (1853). The general form and ornamentation of the latter is indistingusihable from the species described in Section 3 as are the original figures of '*P.*' *Maltonensis* Young and Bird, '*P.*' *Neumayri* de Gregorio, '*P.*' *anughus* de Gregorio and *C. greenhoughi* Skwarko, the syntypes of



Text fig. 105: *Camptonectes (C.) auritus* – posterior hinge length/length.

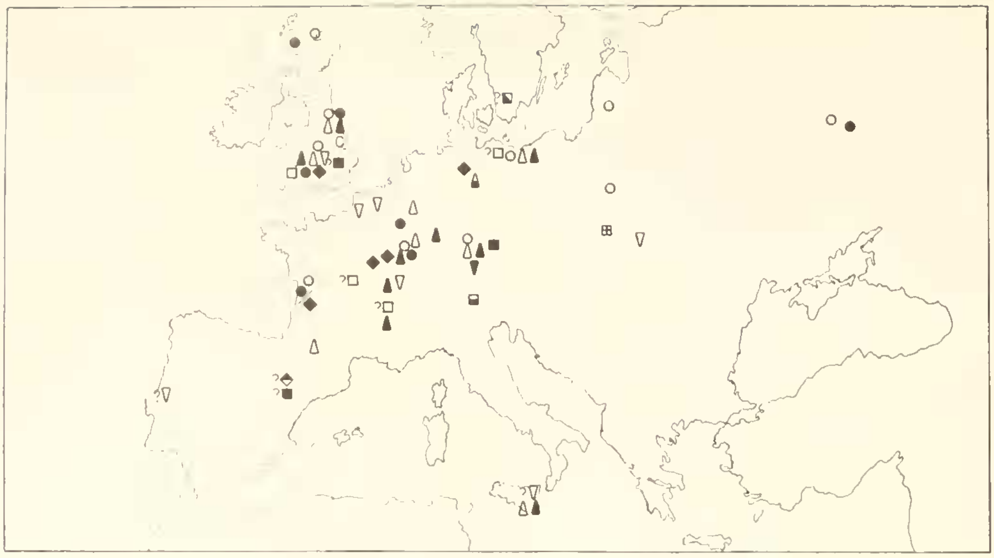
'*P.*' *Clypeatus* Witchell (BM L17536; Pl. 3, Fig. 37), and the originals of *C.* sp. Kirkaldy (OUM J17551–3).

'*P.*' *validus* Lindstrom from the Kimmeridgian is apparently a worn example of the species described in Section 3. The general shape and large size (H: 125) allow only that it might be a representative of *C. (Camptochlamys) obscurus*. Sokolov and Bodylevsky (1931) have applied Lindstrom's specific name to forms which undoubtedly belong to the former species. *Chlamys interpunctata* Troedsson is reported to possess '*Camptonectes*-ornament' but since it is derived from the L. Lias it may be a well preserved representative of *C. (C.) subulatus*. Behmel and Geyer's (1966) unillustrated record of '*P.*' *lens* from the Lias seems to refer to a genuine example of the species described in Section 3. Unillustrated Bathonian records of J. Sowerby's species (1) (Quenstedt, 1843; Terquem and Jourdy, 1869; Schlippe, 1888; Semenow, 1896; Greppin, 1898; Cossmann, 1900; Kilian and Guébhard, 1905; Deninger, 1907; Lissajous, 1923; Roman, 1926) must be treated with great caution because of the possibility of confusion for the much more common Bathonian species *C. (C.) laminatus*. Prior to Arkell's (1930a) description and illustration of J. and J. de C. Sowerby's types '*P.*' *lens* was interpreted very broadly. Thus Staesche (1926) not only included forms referable to *C. (C.) laminatus* within his hypodigm for *C. lens* (not the figured specimen) but also regarded forms which the present author places in *C. (Camptochlamys) obscurus* as being separable from *C. lens* only at the varietal level (see p. 137 for a discussion of this and other 'varieties' of '*P.*' *lens*). Morris and Lycett (1853) also misinterpreted J. Sowerby's hypodigms in assigning coarsely ornamented Bathonian specimens (= *C. (C.) laminatus*) to '*P.*' *lens* and '*P.*' *arcuatus* (2) while Quenstedt (1858, pl. 59, fig. 3) included a specimen with radial striae (= *C. (Cc.) obscurus*) within his hypodigm for '*P.*' *lens*.

Even following Arkell's revision, J. Sowerby's hypodigms have been misinterpreted. Thus Leanza (1942) refers to '*P.*' *(C.) lens* a specimen from the Lias of Argentina which has radial rather than divaricate striae and an abnormally high H/UA (25). A Bathonian specimen (pl. 4, figs. 9, 9a) referred to *C. lens* by Dechaseaux (1936) has the coarse ornament of *C. (C.) laminatus* although another (pl. 4, fig. 11) appears to be a genuine example of *C. lens*. Specimens from the Bathonian referred to '*P.*' *(Camptonectes) lens* by Stoll (1934) very probably belong in *C. (C.) laminatus*.

Other secondary references to synonymous species which are based on specimens which may be outside the range of the species described in Section 3 include '*P.*' *lens* J. Sowerby; Lahusen and '*P.*' *(C.)* cf. *lens* J. Sowerby; Sokolov and Bodylevsky (both based on specimens with strong comarginal ornament which may belong in *C. (Cc.) obscurus*), '*P.*' *(C.) arcuatus* J. Sowerby; Kilian and Guebhard (based on unfigured Bathonian specimens probably referable to *C. (C.) laminatus*) and *C. aalensis* Paris and Richardson; Wandel (based on a specimen (26) with abnormally high H/UA). The specimens referred to d'Orbigny's species *P. Midas* (12) by Dollfus (1863), Damon (1880) and Arkell (1931a) are clearly representatives of late populations of *Radulopecten fibrosus*. With the evident possibility of confusion inadequately characterised references to d'Orbigny's species in de Loriol et al. (1872) and de Loriol and Pellat (1875) cannot confidently be synonymised with the species described in Section 3. The specimen figured as '*P.*' *Buchi* Roemer by de Loriol (1894) has an abnormally high H/UA (27) and is referable to *C. (C.) virdunensis*.

Schlotheim's (1813) '*Chamites*' *auritus*, which was founded on the figure of *Pectinites* in Lister (1678), itself a copy of the figure (discussed above) in Plot (1676), provides the earliest available specific name for the species described in Section 3. Duff (1978: 66) has designated an appropriate neotype. In the interests of brevity secondary references to synonymous species are excluded from the synonymy except where they differ from the original hypodigm or are of relevance to Sections 5–10. Further citations may be traced either directly or through synonymy lists in v. Zieten (1833),



Text fig. 106: *Camptonectes (C.) auritus* – European distribution.

Text fig. 107: *Camptonectes (C.) auritus* – World distribution (Callovian reconstruction).

Roemer (1836), v. Buch (1839), Bronn (1852), Quenstedt (1852), Oppel (1858), Contejean (1859), Waagen (1867), de Loriol and Pellat (1875), Whidborne (1883), Fiebelkorn (1893), Parona (1895), Cossmann (1914), Paris and Richardson (1916), Lewinski (1923), Staesche (1926), Arkell (1930a), Dechaseaux (1936) and Duff (1978).

5. STRATIGRAPHIC RANGE

The earliest record of C. *(C.) auritus* is a single specimen from the Planorbis zone (Hettangian) of S. Germany (Staesche, 1926). Specimens from the L. Lias of Sweden (Troedsson, 1951) and the M. and U. Lias of Spain (Behmel and Geyer, 1966) may be conspecific and specimens from undifferentiated Lias in the Alps (Tausch, 1890) are almost certainly conspecific (see Section 4). A number of examples, reaching a maximum height of 33 mm, are preserved on a block from the Posidonienschiefer (L. Toarcian) of S. Germany (BSPHG) but only one specimen from Northants (BM L89415; Pl. 3, Fig. 36) is recorded in the U. Toarcian.

The species becomes locally very common in the Aalenian and Bajocian but is exceedingly rare in the Bathonian. The following Bathonian specimens in the BM are probably referable to C. *(C.) auritus*: L24155, L24156, L74364, L76505 and L97129. Probable Bathonian records from France (Dechaseaux, 1936) and Greenland (Donovan, 1953) together with a number of dubious records are discussed in Section 4.

In suitable facies C. *(C.) auritus* is found in all stages to the Tithonian and Kelly (1977) records the species from the Ryazanian stage in the Cretaceous of E. England.

6. GEOGRAPHIC RANGE

C. (C.) auritus is much more common in the northern parts of the European region (text fig. 106) but this is probably a reflection of the northerly distribution of the appropriate facies (see Section 8) rather than an indication of a temperature dependance. Outside Europe (text fig. 107) the species has a palaeolatitudinal range of about 150° (maximum of 100° [Kimmeridgian] in any one stage). After the L. Jurassic *C. (C.) auritus* appears to have attained an almost worldwide distribution although there are doubts about records from N. America and the E. Indies (see Section 4) and no known occurrences in S. America. The fact that *C. (C.) auritus* is only known from one locality (E. Greenland; Donovan, 1953) in the Bathonian outside Europe makes it implausible to attribute the extreme rarity of the species at that time within Europe (see Section 5) to a migration elsewhere.

7. DESCRIPTION OF ECOLOGY

C. (C.) auritus occurs in a wide variety of facies in the Aalenian of Europe. It is particularly common in the Northampton Sand Ironstone (Opalinum zone), a chamosite oolite containing a diverse fauna (see p. 26). It is also common in oolitic and pisolitic limestones of the Murchisonae zone in the Cotswolds where it reaches a maximum height of 52 mm (OUM J1913).

In the Bajocian of Yorkshire the species occurs abundantly at certain impure limestone horizons in the Scarborough Formation. The fauna is restricted (dominated by *Gervillella* together with *Cucullaea, Astarte, Cloughtonia* and *Pseudomelania)* and *C. (C.) auritus* is characteristically small (maximum height 43 mm; YM 531a) and has a low H/UA ratio. In the Millepore Bed, a sideritic sandstone with a more diverse fauna (the above together with *Trigonia, Pholadomya*, bryozoa, crinoids and regular echinoids), *C. (C.) auritus* is less common but reaches a maximum height of 72.5 mm (YM 531a). Similarly large sizes are reached by the species in the fully marine Bajocian deposits of S. Germany.

The species is extremely rare in the Bathonian (see Section 5), when *C. (C.) laminatus* is common, and is also rare in the argillaceous facies widely developed in the Callovian. However, in more littoral shallow water facies such as the limestones and sandstones of Yorkshire (U. Cornbrash, Kellaways Rock, Hackness Rock), Scotland (Brora Roof Bed), Poland and the Baltic Region *C. (C.) auritus* is locally common and reaches a maximum height of 61 mm (MNO 3399).

In the Oxfordian the species is found in a variety of shallow water, level bottom environments but appears to show a preference for oolites (e. g. Malton Oolite, Yorkshire). Contrary to Arkell's opinion (1930a) the species is seldom abundant as is demonstrated by the fact that it contributes to none of the trophic nuclei of the benthic faunal associations studied by Fürsich (1977). Oxfordian *C. (C.) auritus* is always found with a high diversity fauna and the maximum height attained is 150 mm (OUM J2361).

The species is not common in the L. Kimmeridge Clay (Kimmeridgian) but in the more marginal sandy facies developed in the upper part of the formation (M. Tithonian) in England (Hartwell Clay) and N. W. France (Assises de Croi) it is locally abundant. Maximum size (H: 34, BM L35267) is, however, small and the H/UA ratio is generally low. *Inoperna* is a particularly common faunal associate.

In the U. Tithonian *C. (C.) auritus* accurs in algal limestones (Townson, 1971) in Portland and the Boulonnais where it reaches a maximum height of 26 mm (BM L52436). The species is rare in more open marine deposits where *C. (Camptochlamys) obscurus* is common.

A few specimens are recorded from the Purbeck beds near Oxford (Kirkaldy, 1963).

The above description concentrates on the common and unusual occurrences of *C. (C.) auritus*. Specimens may in fact be found at almost all horizons in the M. & U. Jurassic of Europe. Notable exceptions, additional to those discussed above and in Section 5, are the Oxfordian-Tithonian coral reef facies of central and southern Europe, where almost all specimens of *C. (Camptonectes)* are referable to *C. (C.) virdunensis* (see p. 131), and the deep water pelagic limestone facies of the M. and U. Jurassic in the peri-Mediterranean region where there is only one doubtful record (Gemmellaro and Di Blasi, 1874; see Section 4), and that from a probable submarine high.

8. INTERPRETATION OF ECOLOGY

It is clear from Section 7 that *C. (C.) auritus* was a remarkably eurytopic species. Although the soft or soupy substrates characteristic of clay or limemud deposition were not apparently suitable, almost all other substrates, including shifting oolite shoals, were colonised. The species was also able to tolerate environments of high physical stress. Thus it is found in Tithonian algal limestones which were probably deposited in very shallow sub-tidal or inter-tidal situations (Sellwood, 1978) where exposure and wave disturbance must have been frequent. Hallam (1976) has also suggested that *Camptonectes* was able to tolerate salinities within the upper brachyhaline regime (24–30‰) and the occurrence of *C. (C.) auritus* in the Purbeck formation, a sequence of marine, lagoonal and freshwater beds (Anderson and Bazley, 1971), supports this general thesis (but see p. 113). While the records of *C. (C.) auritus* are probably from the most fully marine horizons, the lack of any other pectinids suggests that salinity was liable to at least short-term fluctuations. Although ammonites do occur in the Scarborough Formation the reduced faunal diversity of the beds containing *C. (C.) auritus* is generally suggestive of low environmental stability, with perhaps a higher incidence of storms being of controlling importance rather than salinity variations. Jordan (1971) has reinterpreted the Kimmeridgian/Tithonian sequence of L. Saxony in terms of increasing rather than decreasing salinity so the lack of *C. (C.) auritus* suggests that euryhalinity did not extend to a tolerance of hypersaline conditions. However, somewhat rare occurrences of the species in bituminous shales in the L. Toarcian (see Section 5) and M. Callovian (Duff, 1978) suggest that *C. (C.) auritus* had some ability to withstand reduced oxygen tension and there is good evidence of an ability to tolerate various temperatures (see Section 6).

Although a eurytopic species, the size, shape and numbers of *C. (C.) auritus* seem to have been considerably influenced by the environment. Open marine situations characterised by a high diversity fauna supported small populations of large individuals with a high H/UA ratio. Marginal marine environments with a lower diversity fauna supported larger populations of relatively small individiduals with a low H/UA ratio. At first sight the correlation of size and numbers with distance from shoreline suggests that the species could adopt a range of adaptive strategies within the 'K-r' spectrum to allow colonisation of both biologically accommodated and physically controlled biofacies. However, the pattern of shape variation is not in accordance with this interpretation. Since umbonal angle increases during ontogeny one may conclude that individuals with a low H/UA ratio (from marginal marine situations) have grown more slowly, in complete contradiction to the normal policy of 'r' strategists. This might be explained by a strong correlation between shape and developmental stage, in which case precocious maturation and short life span could be invoked for marginal marine populations. This hypothesis could be tested by an analysis of growth lines. In the present absence of data for the latter and with support for the hypothesis from the evolution of *C. (C.) auritus* (see Section 10), the author prefers to adopt the view that marginal marine populations are stunted as a result of high environmental stress. It is suggested that the anomalously large number of individuals may be the consequence of a reduced incidence of predation, as has been demonstrated in Recent shallowwater communities by Jackson (1974).

A close Recent morphological analogue of *C. (C.) auritus* is *Cyclopecten vitrea* (Gmelin), a bathyal species (Knudsen, 1970). The frequent association of *C. (C.) auritus* with endobyssate mytiloid and pterioid bivalves suggests that *Chlamys varia* (Linnaeus), which is found attached to the Horse Mussel *Modiolus modiolus* (A. Brand, pers. comm., 1976), may be a closer Recent ecological analogue than *Cy. vitrea*.

The paucity of *C. (C.) auritus* in open marine environments in the Tithonian may be explained by competition with *C. (Camptochlamys) obscurus*, which is common in such environments. The species are not known to coexist in numbers at earlier horizons. The rarity of *C. (C.) auritus* in reef facies in the U. Jurassic and in all facies in the Bathonian may also be explained by competition (with respectively *C. (C.) virdunensis* and *C. (C.) laminatus*). However, the cause of the rarity of *C. (C.) auritus* in the L. Jurassic is more easily attributed to the widespread development of unfavourable argillaceous facies than to competition with the common species *C. (C.) subulatus*.

9. FUNCTIONAL MORPHOLOGY

The existence of a moderate to large byssal notch indicates that *C. (C.) auritus* was byssally attached, at least early in ontogeny. Adult individuals, especially of later populations, probably gained stability mainly by virtue of their relatively heavy shells.

The thin shell, low convexity, subdued ornamentation and ontogenetic increase in umbonal angle of *C. (C.) auritus* indicate that swimming was a possibility. Phyletic reduction in the rate of H/UA increase, facilitating escape from predators by swimming at larger body sizes, is probably causally related to a parallel increase in maximum height.

Seilacher (1972) has suggested that the apparent difficulty of programming the growth of divaricate ornament must imply great functional significance where it is present. In this respect one might argue that '*Camptonectes*-ornament' provides reinforcement for a thin and therefore weak shell. However, Seilacher also argues that variability should be low in functional structures thus the great variation in the ornament of *C. (C.) auritus* presents a paradox. This could be resolved by invoking individual adaptation and an analysis of the development of ornament along the lines adopted for *Radulopecten vagans* (see Johnson, 1981) might be used to explore this possibility.

10. ORIGINS AND EVOLUTION

Since *C. (C.) auritus* is found in the Planorbis zone its origins may lie outside the Jurassic. True '*Camptonectes*-ornament' is however unknown in the Triassic, the striking ornament exhibited by *Filopecten filosus* (v. Hauer) being the nearest approach to it (see Allasinaz, 1972, pl. 40, figs. 1–7, pl. 41, figs. 1–3).

Insufficient data is available to assess the extent of phyletic evolution within L. Jurassic *C. (C.) auritus*. However, in M. & U. Jurassic representatives evolution is apparent in several characters although the variability of the species does not make for accurate documentation.

Oxfordian populations exhibit a slower rate of increase in PH, t_L and t_R with respect to length than their Bajocian ancestors. In the latter at least PH/L and t_L/L increase during ontogeny thus Oxfordian populations may have evolved by the retardation of shape development relative to size. In the absence of absolute age data it is impossible to say whether later representatives have actually developed more slowly or simply grown faster. In each of the preceding cases the paucity of data from intermediate stages precludes an evaluation of the tempo of evolution. However, data for maximum height is available from a number of levels and seems to indicate an oscillatory pattern in an overall increase from Aalenian to Oxfordian (Aalenian, 52 mm; Bajocian, 72.5 mm; Callovian, 61 mm; Oxfordian, 150 mm). In fact the low Callovian value may well be an artefact of the limited number of museum specimens available for measurement from the stage thus maximum height could exhibit a smooth increase. The marked reversal to the trend in the Tithonian (H_{max}: 34) could also be due to limited data but is more probably the result of stunting (through restriction of the species to high stress environments, see Section 8).

Phyletic increase in size and retardation of somatic development are indicative of 'K' selection (Gould, 1977). This provides further evidence for the view that individuals of small size with low H/UA from marginal marine situations are the products of stunting rather than facultative progenesis (see Section 8). Progenesis appears to be correlated with 'r' selection yet even late, 'K' selected, populations of *C. (C.) auritus* may exhibit small size and a low H/UA.

Camptonectes (Camptonectes) laminatus (J. Sowerby 1818)

Pl. 4, Figs. 10, 12–16, ?Fig. 11; text figs. 108–117

Synonymy

v* 1818 *Pecten laminata* sp. nov; J. Sowerby, p. 4, pl. 205, fig. 4.
v* 1818 *Pecten similis* sp. nov; J. Sowerby, p. 5, pl. 205, fig. 6.

1818 *Pecten rigida* sp. nov; J. Sowerby, p. 5, pl. 205, fig. 8.

1850 *Pecten Langrunensis* sp. nov; d'Orbigny, v. 1, p. 314 (Boule, 1912, p. 93).

1853 *Pecten Woodwardii* sp. nov; Morris and Lycett, p. 8, pl. 1, fig. 20.

1853 *Pecten arcuatus* J. Sowerby; Morris and Lycett, p. 11, pl. 1, fig. 18 (non J. Sowerby sp.).

1853 *Pcten lens* J. Sowerby; Morris and Lycett, p. 11, pl. 2, figs. 1, 1a (non J. Sowerby sp.).

1863 *Pecten rigidus* J. Sowerby; Lycett, p. 31, pl. 40, fig. 16.

v* 1869 *Pecten anguliferus* sp. nov; Terquem and Jourdy, p. 128, pl. 13, fig. 16.

1871 *Pecten divaricatus* sp. nov; Phillips, p. 240, pl. 11, fig. 29.

1883 *Pecten puellaris* sp. nov; Whidborne, p. 501, pl. 19, figs. 3, 3a.

1905 *Pecten (Camptonectes) rigidus* J. Sowerby; Kilian and Guébhard, p. 758.

1905 *Pecten (Camptonectes) rigidus* J. Sowerby; Kilian and Guébhard, p. 758.

pv 1926 *Camptonectes lens* (J. Sowerby); Staesche, p. 76, pl. 2, fig. 8 (non J. Sowerby sp.).

1932 *Camptonectes rigidus* (J. Sowerby); Spath, p. 113, pl. 5, fig. 4, pl. 10, fig. 5.

? 1933 *Pecten (Chlamys) curvivarians* sp. nov; Dietrich, p. 63, pl. 81, figs. 122, 123.

v 1936 *Camptonectes lens* (J. Sowerby); Dechaseaux, p. 30, pl. 4, figs. 9, 9a (non figs. 11, 14, non J. Sowerby sp.).

p 1948 *Camptonectes laminatus* (J. Sowerby); Cox and Arkell, p. 13.

1948 *Camptonectes rigidus* (J. Sowerby); Cox and Arkell, p. 13.

? *1950* *Camptonectes laminatus* (J. Sowerby); Channon, p. 248.

non 1952 *Chlamys curvivarians* (Dietrich); Cox, p. 8, pl. 2, figs. 5, 8.

1953 *Camptonectes* cf. *laminata* (J. Sowerby); Marwick, p. 100, pl. 10, fig. 11.

1959 *Camptonectes inexpectatus* sp. nov; Hayami, p. 70, pl. 7, figs. 4, 5.

? 1961 *Camptonectes rigidus* (J. Sowerby); Rossi Ronchetti and Fantini Sestini, p. 122, pl. 13, figs. 1, 2.

1961 *Camptonectes* sp; Rossi Ronchetti and Fantini Sestini, p. 123, pl. 13, fig. 4.

1964 *Camptonectes laminatus* (J. Sowerby); J.-C. Fischer, p. 18.

1964 *Camptonectes rigidus* (J. Sowerby); J.-C. Fischer, p. 19.

1964 *Camptonectes plattessiformis* (White); Imlay, p. 26, pl. 2, figs. 11–14.

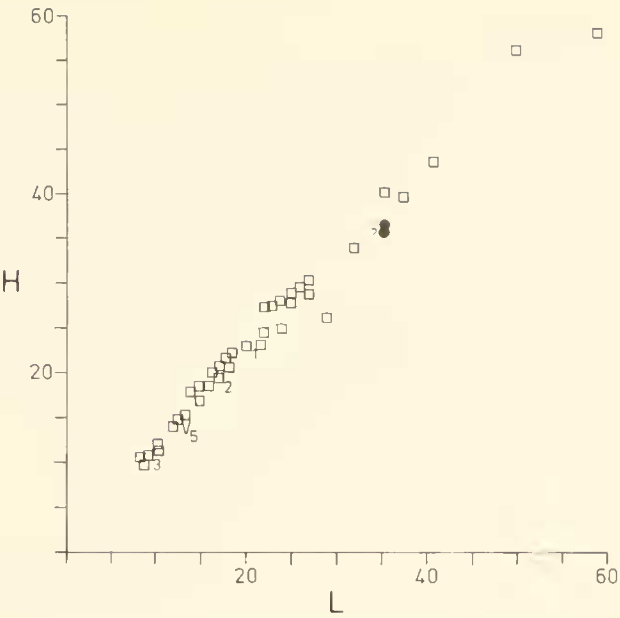
1967 *Camptonectes platessiformis* (White); Imlay, p. 79, pl. 2, figs. 1, 2.

p 1978 *Camptonectes laminatus* (J. Sowerby); Bradshaw, p. 313.

Holotype (M) of *Pecten laminata* J. Sowerby 1818, p. 4, pl. 205, fig 4; BM 43327; Pl. 4, Fig. 14 herein; Forest Marble (see Arkell, 1930a: 96) or L. Cornbrash (both Bathonian), Chatley Lodge, Somerset.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

'Spec Char. Suborbicular, depressed, striated; striae arched, diverging: ears triangular, unequal; the largest plaited.



Text fig. 108: *Camptonectes (C.) laminatus* – height/length.

The striae are slightly undulated; to the naked eye they appears smooth, but when carefully examined with a lens, minute lines may be traced across them. The plaits upon the ear form a strong character, whence the name.

In shelly limestone (Cornbrash) at Chatley Lodge, in Somersetshire.'

2. AMENDED DIAGNOSIS

Distinguished from all other species of *C. (Camptonectes)* by the coarseness of the divaricate ornament on the disc and the strength of the comarginal lamellae on the anterior auricle of the left valve.

3. AMENDED DESCRIPTION

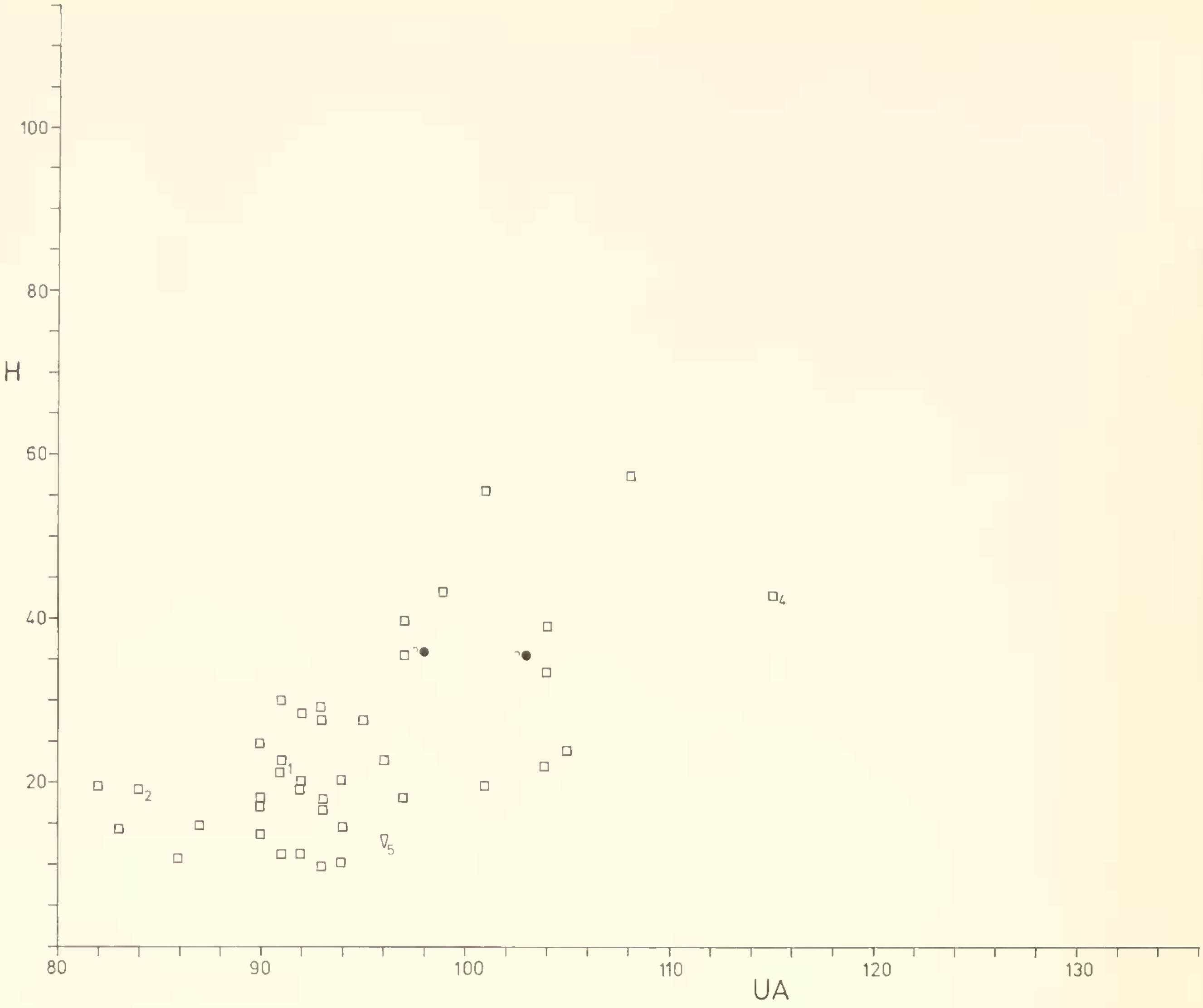
Essentially similar to *C. (C.) auritus* except for the diagnostic features (see Section 2), smaller maximum height (59.5 mm, Imlay, 1964), apparent allometric decrease in N/L (text fig. 112) and somewhat thicker shell. The remaining metric proportions are plotted in text figs. 108–111, 113–115, while the range of ornamental variation is depicted in Pl. 4, Figs. 10, 12–16.

4. DISCUSSION

The holotypes (M) of:

1. *'Pecten' laminata* J. Sowerby (BM 43327; Pl. 4, Fig. 14) and
2. *'P.' similis* J. Sowerby (BM 43329; Pl. 4, Fig. 12) and the sole observed type of:
3. *'P.' anguliferus* Terquem and Jourdy (ENSM L334; Pl. 4, Fig. 16)

are indistinguishable from the species described in Section 3 on the basis of metric proportions and ornament. The original figure of *Camptonectes* sp; Rossi Ronchetti and Fantini Sestini (4) is similarly inseparable.

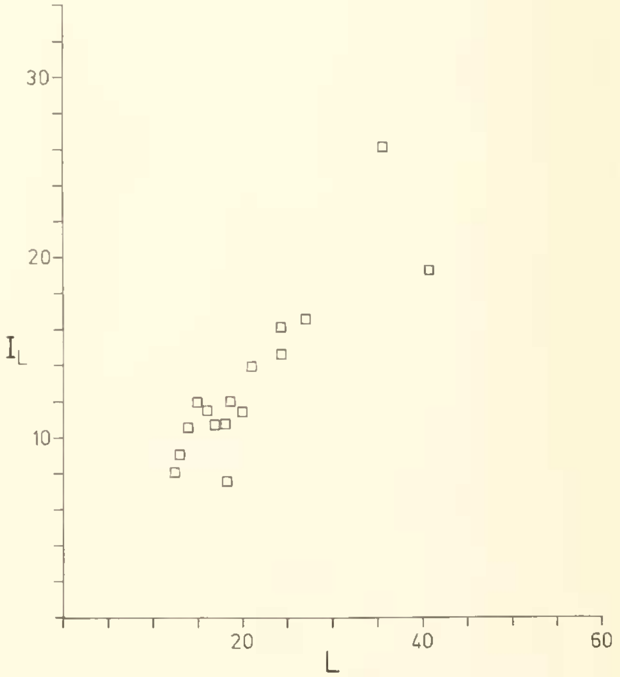


Text fig. 109: *Camptonectes (C.) laminatus* – height/umbonal angle.

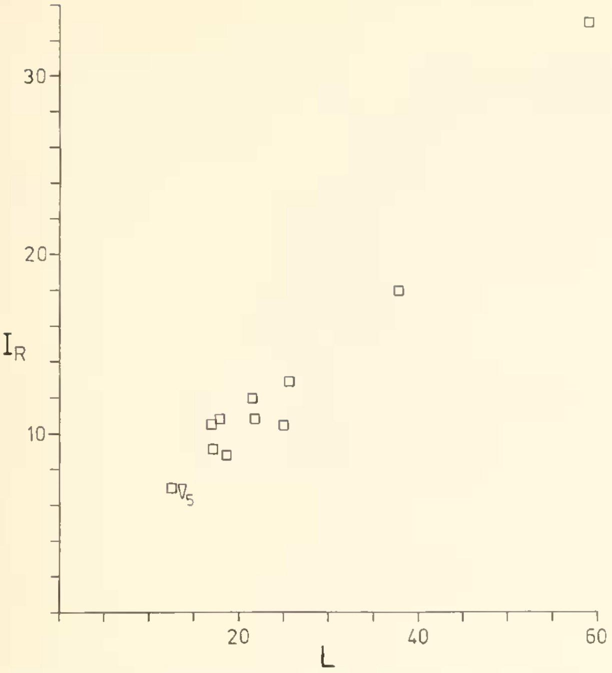
Since the number of divaricate striae increases during the ontogeny of the species described in Section 3, species erected for small specimens with relatively few striae (*'P.' rigida* J. Sowerby, *'P.' Langrunensis* d'Orbigny, *'P.' Woodwardii* Morris and Lycett, *'P.' divaricatus* Phillips, *'P.' puellaris* Whidborne) cannot be accorded a distinction.

Although not from the typical horizon of derivation (Bathonian) there seems no reason to separate *C. platessiformis* White; Imlay (from the Bajocian of the U. S. Western Interior) and *C. inexpectatus* Hayami (from the L. Lias of Japan) from the species described in Section 3. Both have the coarse divaricate striae and auricular lamellae characteristic of the latter species and the comarginal ornament of the disc seems too weak to allow any possibility that *C. platessiformis* and *C. inexpectatus* might be representative of *C. (Camptochlamys) obscurus*.

The original figure of *'P.' (Chlamys) curvivarians* Dietrich depicts a specimen which resembles the species described in Section 3 in its divaricate ornament and all metric proportions apart from H/UA (5). However, Cox (1952) refers specimens with very much stronger ornament to Dietrich's species and since the stratigraphic range of the latter (Bajocian-Tithonian) extends to considerably younger horizons than that of the



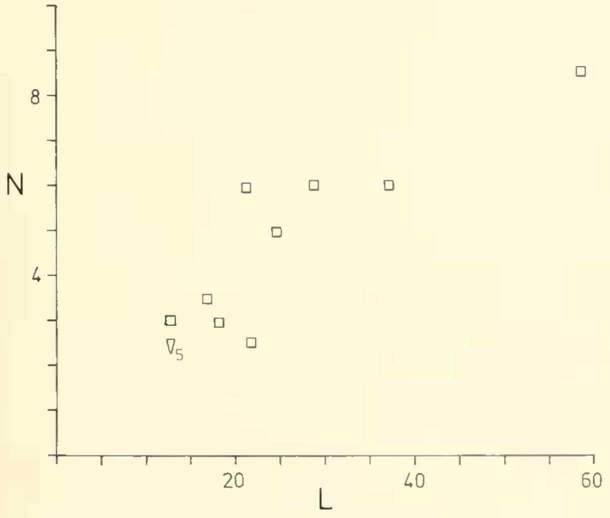
Text fig. 110: *Camptonectes (C.) laminatus* – intersinal distance on left valve/length.



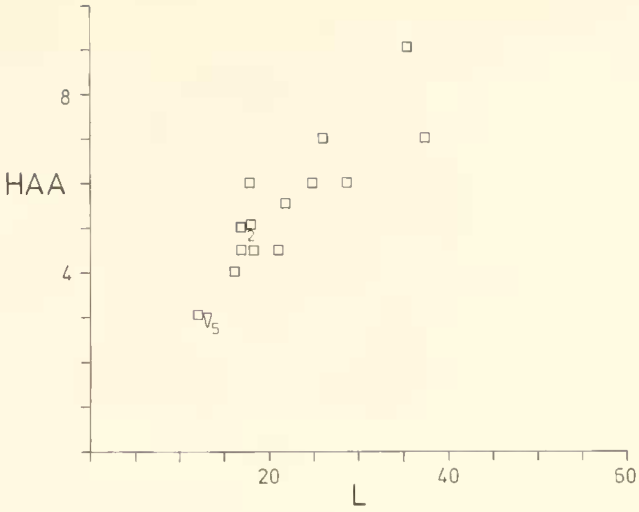
Text fig. 111: *Camptonectes (C.) laminatus* – intersinal distance on right valve/length.

species described in Section 3 it is probable that they are distinct.

Of the synonymous species discussed above the earliest available name for the species described in Section 3 is *'P.' laminata* J. Sowerby. Both Cox and Arkell (1948) and Channon (1950) refer unfigured Aalenian and Bajocian specimens from the Cotswolds to *C. laminatus*. Since J. Sowerby's species is extremely rare in the latter stages in England it is likely that they in fact belong to the much more common species *C. (C.) auritus*. Conversely Bathonian records of junior synonyms of *C. (C.) auritus* (listed under the latter species) in Quenstedt (1843), Terquem and Jourdy (1869), Schlippe (1888), Semenow (1896), Greppin (1898), Cossmann (1900), Kilian and Guébhard (1905), Deninger (1907), Lissajous (1923) and Roman (1926) may well refer to *C. (C.) laminatus* and some of the Bathonian specimens referred to junior synonyms of *C. (C.) auritus* (see p. 121) in Morris and Lycett (1853), Staesche (1926) and Dechaseaux (1936) undoubtedly belong to *C. (C.) laminatus*.



Text fig. 112: *Camptonectes (C.) laminatus* – depth of byssal notch/length.

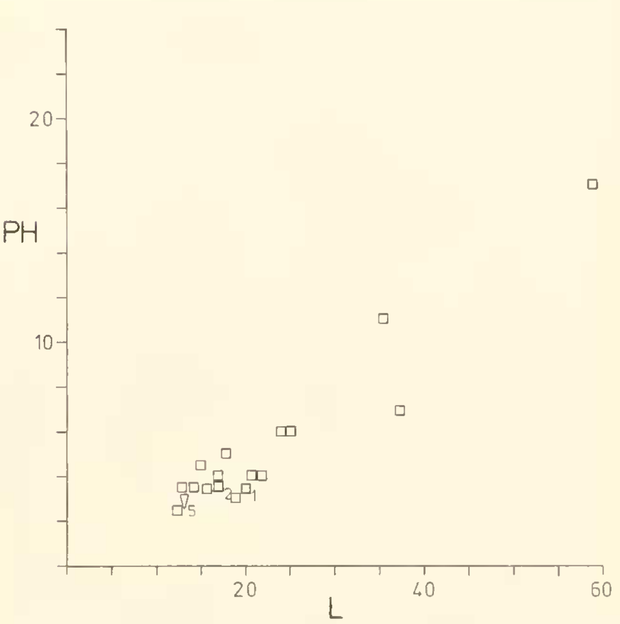


Text fig. 113: *Camptonectes (C.) laminatus* – height of anterior auricle/length.

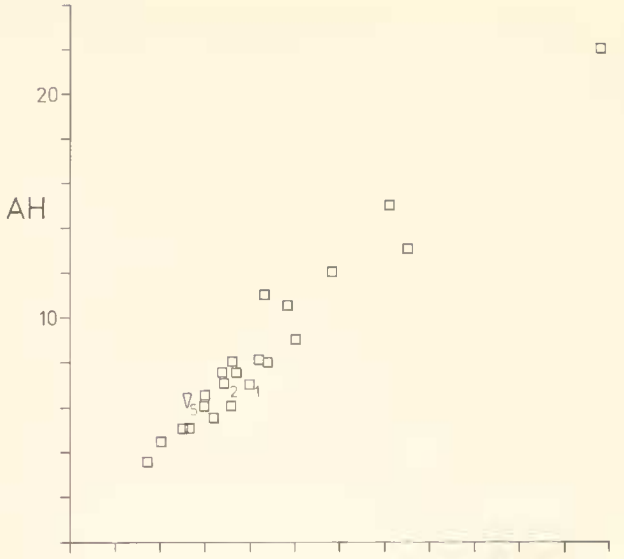
The original figure of *C. rigidus* (J. Sowerby); Rossi Ronchetti and Fantini Sestini depicts a specimen with radial rather than divaricate striae which is thus probably referable to *C. (Camptochlamys) clathratus* rather than *C. (C.) laminatus*. Bradshaw's (1978) inclusion of specimens with strong comarginal ornament within *C. laminatus* indicates that his hypodigm probably extended to forms which the present author places in *C. (Camptochlamys) obscurus*.

5. STRATIGRAPHIC RANGE

The earliest record of *C. (C.) laminatus* is from the L. Lias of Japan (Hayami, 1959). Thenceforth, apart from dubious records from the Aalenian of the Cotswolds (see Section 4),



Text fig. 114: *Camptonectes (C.) laminatus* – posterior hinge length/length.



Text fig. 115: *Camptonectes (C.) laminatus* – anterior hinge length/length.

the species is unknown until the Bajocian when it is recorded from the U. S. Western Interior (Imlay, 1964, 1967). Only two specimens from the Bajocian of England (BM L47437, L41956) can be definitely referred to *C. (C.) laminatus*. The species becomes common in the Bathonian but thereafter is extremely rare. Records from New Zealand (Marwick, 1953) and Afghanistan (Rossi Ronchetti and Fantini Sestini, 1961) may include Callovian examples while two coarsely ornamented specimens from the Oxfordian of England (BM L20487; LL8339, Pl. 4, Fig. 11) may be referable to *C. (C.) laminatus*.

6. GEOGRAPHIC RANGE

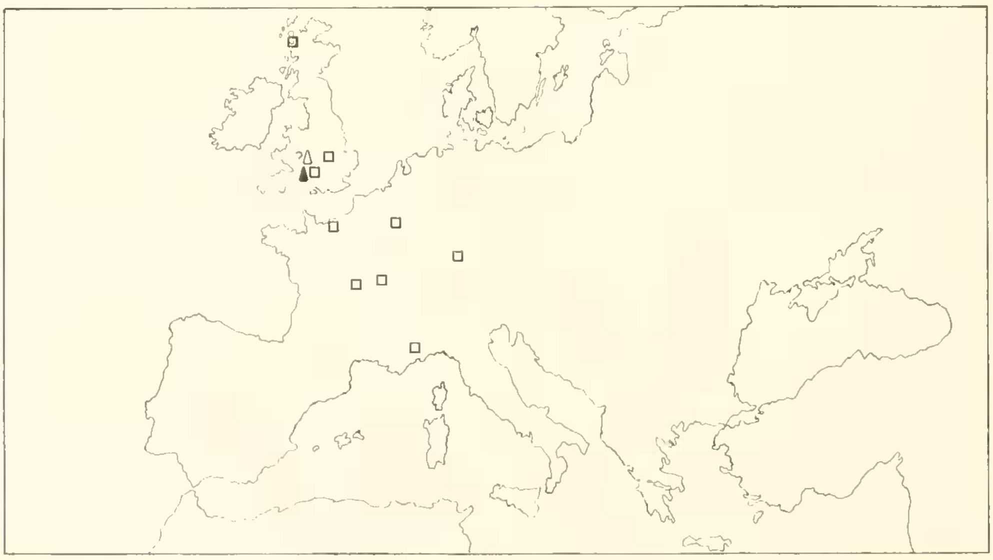
In Europe (text fig. 116) *C. (C.) laminatus* is largely restricted to France and England. Elsewhere (text fig. 117) the species is only known in numbers in the U. S. Western Interior. Since occurrences there (Bajocian) predate common occurrences in Europe (Bathonian) and postdate records of the species in Japan (L. Lias), it may be that *C. (C.) laminatus* undertook an eastward migration, perhaps making use of the marine connection between western America and Europe which was established in Bajocian times (Hallam, 1975a). Viewed in these terms records of the species from the Bathonian-Callovian of New Zealand can be taken to represent a relict population.

7. DESCRIPTION OF ECOLOGY

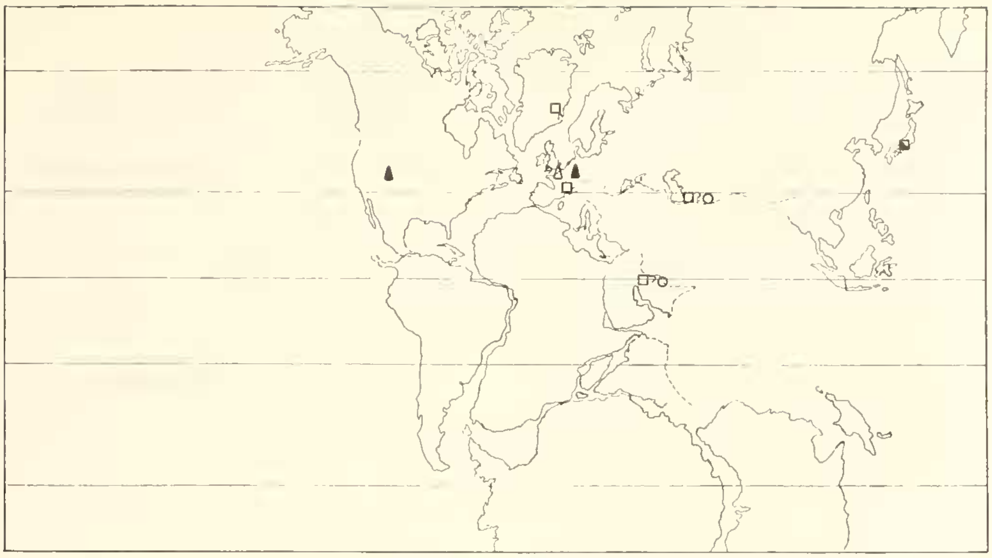
In the Bajocian of the U. S. Western Interior *C. (C.) laminatus* is the only pectinid present in limestones and shales containing a rather restricted fauna, dominated by *'Ostrea' and Vaugonia*. The maximum height attained is 59.5 mm (Imlay, 1964).

In the Bathonian of S. England *C. (C.) laminatus* is recorded from the Minchinhampton Beds (L. Bathonian), shelly oolites containing a diverse fauna, in which the species reaches a maximum height of 58 mm (BM 20744). In the approximately contemporaneous Fuller's Earth Clay on the Dorset coast, fragments of *C. (C.) laminatus* are common in an otherwise almost monotypic bed of *Praeexogyra hebridica*. In the U. Bathonian *C. (C.) laminatus* occurs commonly in the Forest Marble, a grain supported, partly oolitic limestone with a dominantly epibenthic fauna of oysters, *Modiolus* and *Epithyris*. The species is also found in the L. Cornbrash, a non-oolitic, shell-fragment limestone with abundant infaunal bivalves *(Ceratomya, Pleuromya)* and echinoids *(Holectypus, Nucleolites)* in addition to epifaunal bivalves *(Entolium (E.) corneolum, Meleagrinella)* and brachiopods *(Obovothyris)*.

In the Bathonian of central England occasional specimens of *C. (C.) laminatus* are found in paralic clay/limestone sequences in association with a low diversity fauna dominated by *Praeexogyra hebridica* but also containing *Placunopsis, Modiolus, Myopholas, Cuspidaria,* and *Kallirhynchia* (Torrens, 1968). J. D. Hudson (pers. comm., 1977) has recorded a single specimen from similar facies in the Inner Hebrides.



Text fig. 116: *Camptonectes (C.) laminatus* – European distribution.



Text fig. 117: *Camptonectes (C.) laminatus* – World distribution (Callovian reconstruction).

Outside Britain the species appears to be less common but occurs at most levels in the Bathonian. It is not found in the deep water pelagic limestones of the peri-Mediterranean region, the only records from the latter area being from shallow water oolitic deposits (e. g. Kilian and Guébhard, 1905).

8. INTERPRETATION OF ECOLOGY

It is clear from Section 7 that apart from showing a general preference for shallow water environments, *C. (C.) laminatus* was a eurytopic species. Environments supporting a diverse fauna were preferred but in such situations both high energy oobiosparites (e. g. Minchinhampton Beds, Forest Marble) and lower energy biomicrites (e. g. L. Cornbrash) were colonised. The occurrence of *C. (C.) laminatus* in low diversity faunas such as in the Bajocian of the U. S. Western Interior (lacking in *Gryphaea*, pholadomyoids and other pectinids) and the Bathonian of the E. Midlands (lacking in cephalopods, ectoprocts and corals) indicates a tolerance of high environmental stress. In the former case the presence nearby of gypsiferous deposits (Gypsum Springs Formation) indicates that high stress was the result of hypersaline conditions (Hallam, 1975a). However, in the latter case the absence of evaporites suggests that high stress probably resulted from low or fluctuating salinities. The euryhaline oyster *Praeexogyra hebridica* (see J. Hudson and Palmer, 1976) is a frequent associate in the Bathonian of the E. Midlands but M. J. Bradshaw reports (pers. comm., 1977) that *C. (C.) laminatus* is only found, and then rarely, in the beds with the greatest marine influence. The impression thus gained, that *C. (C.) laminatus* was only able to withstand slightly abnormal salinities, is bolstered by the extreme rarity of the species in the Hebrides, where the Bathonian is of generally less marine aspect, and the more frequent occurrence in the *Praeexogyra hebridica* Bed in Dorset where the presence of adherent Foraminifera (and of ammonites in the surrounding clays) suggests nearly normal salinities (J. Hudson and Palmer, 1976).

The frequent association with oysters suggests that *C. (C.) laminatus* may have used this group for byssal attachment.

9. FUNCTIONAL MORPHOLOGY

Since *C. (C.) laminatus* is in most morphological respects identical to *C. (C.) auritus* a similar byssate mode of life can be inferred. The maximum height (59.5 mm) is small enough to suggest that the species was byssate throughout ontogeny. However, the apparent allometric decrease in N/L may indicate that the largest individuals were free living. The more prominent ornament of *C. (C.) laminatus* may have resulted in a stronger shell than *C. (C.) auritus* but this does not appear to correlate with any autecological differences, both species being common in high energy environments.

10. ORIGINS AND EVOLUTION

C. (C.) laminatus almost certainly evolved from *C. (C.) auritus.* The stratigraphically and geographically isolated first occurrence of *C. (C.) laminatus* (L. Lias, Japan), a subsequent migration (see Section 6), and the sudden appearance of the species in Europe are classic indications of allopatric speciation.

Since the number of divaricate striae increases during the ontogeny of *C. (C.) auritus* the relatively widely spaced ornament of *C. (C.) laminatus* may be a product of heterochronic retardation of the rate of ornamental development. The appearance of auricular lamellae cannot, however, be simply explained by heterochrony and suggests that speciation involved at least some change in the structural genome.

There is no evidence for any phyletic evolution within *C. (C.) laminatus.*

The decline and subsequent extinction of *C. (C.) laminatus* is correlated with the reappearance in Europe of large numbers of *C. (C.) auritus.* It may be that after a phase of competitive exclusion in the Bathonian *C. (C.) auritus* had evolved sufficiently (see p. 124) to outcompete *C. (C.) laminatus* in the Callovian and Oxfordian.

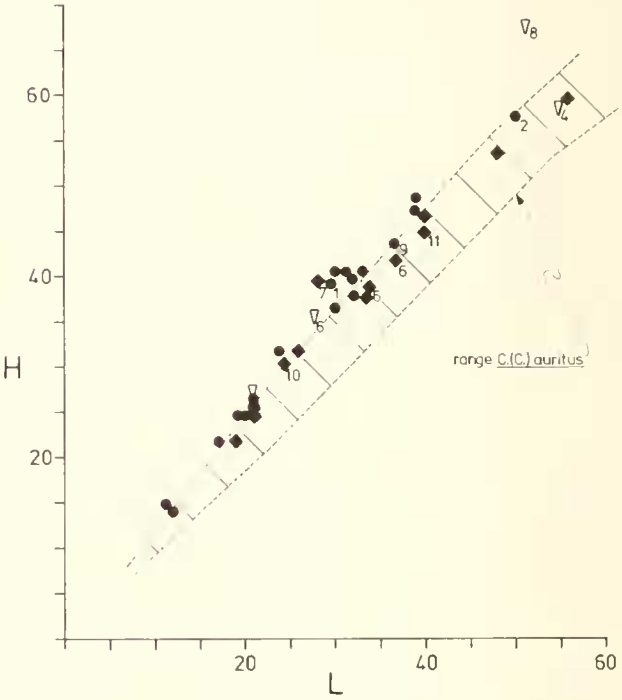
Camptonectes (Camptonectes) virdunensis (BUVIGNIER 1852)

Pl. 4, Figs. 1, 2; text figs. 118–120

Synonymy

? 1852 *Pecten Zieteneus* sp. nov; BUVIGNIER, p. 24, pl. 19, figs. 24, 25.
1852 *Pecten virdunensis* sp. nov; BUVIGNIER, p. 24, pl. 20, figs. 4–6.
? 1852 *Pecten suprajurensis* sp. nov; BUVIGNIER, p. 24, pl. 19, figs. 21–23.
(?) *1859* *Pecten suprajurensis* (BUVIGNIER); CONTEJEAN, p. 218.
? 1859 *Pecten Flamandi* sp. nov; CONTEJEAN, p. 312, pl. 24, figs. 1, 2.
? 1862 *Pecten Delessei* sp. nov; ÉTALLON in THURMANN and ÉTALLON, p. 263, pl. 37, fig. 9.
1862 *Pecten Sahleri* sp. nov; ÉTALLON in THURMANN and ÉTALLON, p. 264, pl. 37, fig. 10.
(?) 1862 *Pecten flamandi* CONTEJEAN; THURMANN and ÉTALLON, p. 264, pl. 37, fig. 1.
? 1862 *Pecten Waldeckensis* sp. nov; ÉTALLON in THURMANN and ÉTALLON, p. 265, pl. 37, fig. 3.
non 1866 *Pecten suprajurensis* BUVIGNIER; DE LORIOL and PELLAT, p. 105, pl. 10, fig. 5.
(?) 1868 *Pecten suprajurensis* BUVIGNIER; DE LORIOL and COTTEAU, p. 644.
1872 *Pecten suprajurensis* BUVIGNIER; DE LORIOL et al., p. 379, pl. 22, fig. 3.
1874 *Pecten titonius* sp. nov; GEMMELLARO and DI BLASI, p. 120, pl. 3, figs. 13–15.
(?) 1875 *Pecten suprajurensis* BUVIGNIER; DE LORIOL and PELLAT, p. 188.
? 1875 *Pecten Flamandi* CONTEJEAN; DE LORIOL and PELLAT, p. 194, pl. 22, figs. 6, 7.
1875 *Pecten virdunensis* BUVIGNIER; DE LORIOL and PELLAT, p. 199, pl. 22, fig. 16.
1881a *Pecten* aff. *tithonius* GEMMELLARO and DI BLASI, BOEHM, p, 183, pl. 40, fig. 5.
1882 *Pecten (Camptonectes) virdunensis* BUVIGNIER; ROEDER, p. 55.
v 1883 *Pecten tithonius* GEMMELLARO and DI BLASI; BOEHM, p. 605, pl. 67, figs. 21–23.
1894 *Pecten Buchi* ROEMER; DE LORIOL, p. 53, pl. 6, fig. 7 (non ROEMER sp.).
1903 *Pecten tithonius* GEMMELLARO and DI BLASI; REMES, p. 201.
1904 *Pecten (Camptonectes) ledonicus* sp. nov; DE LORIOL, p. 227, pl. 24, fig. 2.
v 1905 *Pecten virdunensis* BUVIGNIER; PERON, p. 223.
vp 1905 *Pecten zieteneus* BUVIGNIER; PERON, p. 224.
v 1905 *Pecten suprajurensis* BUVIGNIER; PERON, p. 229.
? 1914 *Chlamys virdunensis* (BUVIGNIER); COSSMANN, p. 2, pl. 5, fig. 1.
? 1920 *Pecten tithonius* GEMMELLARO and DI BLASI; FAURE-MARGUERIT, p. 56.
1925 *Pecten virdunensis* BUVIGNIER; ROMAN, p. 194.
1926 *Pecten tithonius* GEMMELLARO and DI BLASI; STAESCHE, p. 82, pl. 5.
1930a *Camptonectes virdunensis* (BUVIGNIER); ARKELL, p. 99, pl. 7, figs. 5, 5a.
(?) 1935 *Chlamys suprajurensis* (BUVIGNIER); SALIN, p. 140.
1936 *Camptonectes ledonicus* (DE LORIOL); DECHASEAUX, p. 34, pl. 5, fig. 3.
non 1936 *Camptonectes Zietenus* (BUVIGNIER); DECHASEAUX, p. 34, pl. 5, figs. 5, 6.
1936 *Camptonectes Virdunensis* (BUVIGNIER); DECHASEAUX, p. 34, pl. 5, fig. 4.
(?) 1936 *Camptonectes Flamandi* (CONTEJEAN); DECHASEAUX, p. 35.
(?) 1936 *Camptonectes suprajurensis* (BUVIGNIER); DECHASEAUX, p. 36.
non 1936 *Camptonectes suprajurensis* (BUVIGNIER); SPATH, p. 106, pl. 41, figs. 2–4, pl. 42, fig. 9, pl. 43, fig. 4.
1939 *Camptonectes virdunensis* (BUVIGNIER); STEFANINI, p. 175, pl. 19, fig. 13.
v 1975 *Camptonectes (Camptochlamys) tithonius* (GEMMELLARO and DI BLASI); YAMANI, p. 55.

The type material of *Pecten Virdunensis* BUVIGNIER 1852, p. 24, pl. 20, figs. 4–6 may be in NM. The material was derived from the U. Oxfordian of Verdun (Meuse).



Text fig. 118: *Camptonectes (C.) virdunensis* – height/length.

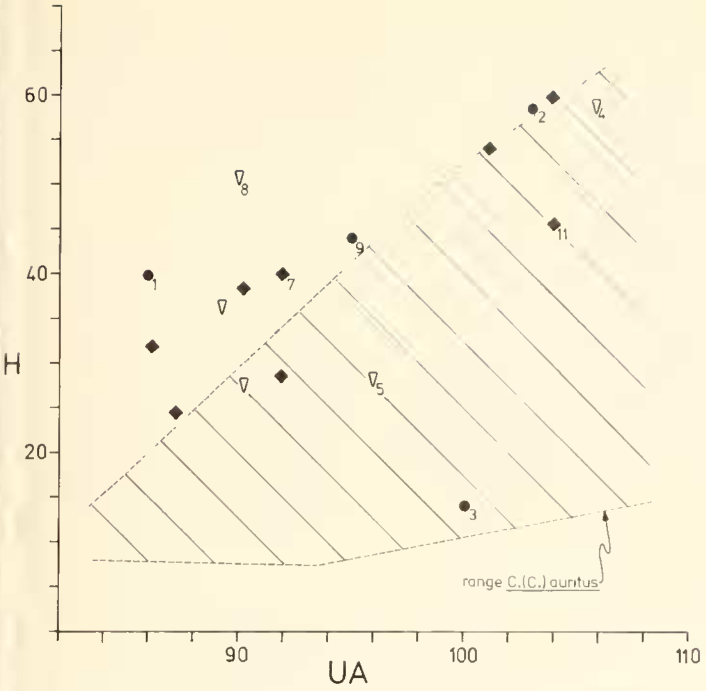
1. ORIGINAL DIAGNOSIS AND DESCRIPTION

'P. testa ovali – elongata, depressa, inaequivalvi, inferne rotundata, superne acuta; concentrice et radiatim striata; striis radiantibus arcuatis, punctulatis, striis concentricis interruptis; valva sinistra convexiori; cardine recto; auriculus posticis, brevibus, obliquis; anticis majoribus.

Longuer 29 mill., hauteur 40, épaisseur 10.

Coquille ovale allongée aplatie, inequivalve, arrondie inférieurement, et (en faisant abstraction des oreillettes) se terminant en pointe vers les crochets, stries rayonnantes arquées, laissant entr'elles des côtes legèrement convexes et se croisant avec des stries concentriques, interrompues sur les côtes, et tres-marquées dans le fond des stries rayonnantes; valve gauche un peu plus bombée que l'autre; charnière droite; oreillettes postérieures courtes et obliques; les antérieures plus allongées; crochets aigus.

Des assises moyennes du coral-rag de Verdun. r.'



Text fig. 119: *Camptonectes (C.) virdunensis* – height/umbonal angle.

2. AMENDED DIAGNOSIS

Distinguished from all other species of *C. (Camptonectes)* by the consistently sub-ovate disc (H >L).

3. AMENDED DESCRIPTION

Essentially similar to *C. (C.) auritus* apart from the diagnostic feature (see Section 2), higher mean H/UA (text fig. 119), apparently isometric growth of H/L (text fig. 118) to the maximum height of 67.5 mm (Gemmellaro and Di Blasi, 1874), somewhat weaker ornamentation and thinner shell. The sub-ovate form is illustrated in Pl. 4, Figs. 1, 2.

4. DISCUSSION

Buvignier's (1852) drawings of '*P.*' *Zieteneus* and '*P.*' *Virdunensis* are both based on specimens derived from U. Oxfordian reef facies. However, only that of '*P.*' *Virdunensis* (1) definitely depicts the narrow *C. (Camptonectes)* species which is common in this facies (see Section 8) and described in Section 3. The dimensions of the figure of *P. Zieteneus* (2) plot within the range of the species described in Section 3 but the figure is an enlargement and Dechaseaux (1936), who probably had access to the original, has referred to *Camptonectes Zietenus* specimens whose dimensions (3) are comparable with *C. (C.) auritus*, of which they would thus seem to be rare representatives from reef facies (see p. 123). Although Peron (1905) has applied the name '*P.*' *zieteneus* to specimens which are at least in part referable to the species described in Section 3, it seems preferable to adopt the name *C. (C.) virdunensis* for the latter until such time as the type material of '*P.*' *Zieteneus* (which would have priority as name bearer) is relocated and shown unequivocally to be representative of the species described in Section 3. The figure of '*P.*' *suprajurensis* Buvignier (4) has metric proportions within the range of *C. (C.) virdunensis* but like that of '*P.*' *Zieteneus* is an enlargement. De Loriol and Pellat (1866) and Peron (1905), who may have had access to the original, have applied the specific name to specimens whose metric proportions (5 and 6 respectively) are comparable with *C. (C.) auritus*. However, de Loriol et al. (1872) figure a specimen which seems to be representative of *C. (C.) virdunensis* under '*P.*' *suprajurensis*. With the evident possibility of confusion the systematic affinities of the type material of '*P.*' *suprajurensis* and of inadequately characterised specimens referred to the species in Contejean (1859), de Loriol and Cotteau (1868), de Loriol and Pellat (1875), Salin (1935) and Dechaseaux (1936) are best left an open question. Specimens referred to *C. suprajurensis* by Spath (1936) can however definitely be placed in *C. (C.) auritus* (see p. 118).

'*P.*' *Sahleri* Étallon, '*P.*' *titonius* Gemmellaro and Di Blasi and '*P.*' *ledonicus* de Loriol are inseparable from *C. (C.) virdunensis* by their metric proportions (respectively 7, 8

Text fig. 120: *Camptonectes (C.) virdunensis* – European distribution.

and 9) and ornament. '*P.*' *Waldeckensis* ÉTALLON is also inseparable by metric proportions (10) and the apparent lack of ornament can probably be attributed to abrasion. The original figure of '*P.*' *Flamandi* CONTEJEAN has H/L (11) very similar to that of *C. (C.) virdunensis* but H/UA is abnormally small. While this might be due to inaccurate drawing the existence of quite strong comarginal ornament in addition to divaricate striae suggests that CONTEJEAN's species may be referable to *C. (Camptochlamys) obscurus*. Specimens figured under '*P.*' *Flamandi* by DE LORIOL and PELLAT (1875) may have similar affinities but those referred to CONTEJEAN's species by THURMANN and ÉTALLON (1862) and DECHASEAUX (1936) almost certainly belong in *C. (C.) virdunensis*.

'*Chlamys*' *virdunensis* (BUVIGNIER); COSSMANN was compared with '*P.*' *clathratus* ROEMER while FAURE-MARGUERIT's (1920) record of GEMMELLARO and DI BLASI's species was based on specimens said to have 'quadrilateral' ornament. This suggests possible misapplication of these specific names to examples of *C. (Camptochlamys)*.

The affinities of '*P.*' *Buchi* DE LORIOL (non ROEMER) and '*P.*' *Delessei* ÉTALLON are discussed under *C. (C.) auritus*.

5. STRATIGRAPHIC RANGE

C. (C.) virdunensis is first recorded in the L. Oxfordian of Alsace (ROEDER, 1882). Thenceforth it is found locally until the U. Tithonian when it is recorded from Stramberg in Czechoslovakia (BOEHM, 1883; REMES, 1903).

6. GEOGRAPHIC RANGE

Common occurrences of *C. (C.) virdunensis* are restricted to the central and southern parts of Europe (text fig. 120) where the appropriate reefal facies (see Section 8) is widespread. The only known occurrence of the species outside Europe is a single specimen from the Oxfordian/Kimmeridgian of Somalia (STEFANINI, 1939).

7. DESCRIPTION OF ECOLOGY

C. (C.) virdunensis is found commonly in the U. Oxfordian coral reef facies if the Yonne (PERON, 1905), where it reaches a maximum height of 49 mm (MNS). The diverse associated fauna is described on p. 88. Contemporaneous occurrences of the species in the Meuse (BUVIGNIER, 1852) and Jura (DE LORIOL, 1894, 1904) are from similar facies.

In the Kimmeridgian *C. (C.) virdunensis* is found in coral reef facies at Kelheim (BOEHM, 1881a) and reef derived facies in the E. Paris Basin where the species reaches a maximum height of 60 mm (NM).

In the L. Tithonian *C. (C.) virdunensis* is recorded from the Nattheim and Neuburg coral reefs in S. Germany (STAESCHE, 1926; YAMANI, 1975). In similar facies in Sicily (GEMMELLARO and DI BLASI, 1874) the species is reported to be common and to attain a maximum height of 67.5 mm.

In the U. Tithonian coral reef at Stramberg *C. (C.) virdunensis* is recorded commonly by BOEHM (1883).

Of the other unequivocal records of *C. (C.) virdunensis* listed in synonymy only those in DE LORIOL and PELLAT (1875), DE LORIOL et al. (1872) and ARKELL (1930a) can be said to refer to specimens which are definitely not derived from reef facies. In the first two cases (from the Kimmeridgian of the Boulonnais and the 'Portlandian' of the E. Paris Basin respectively) the number of specimens is indeterminate and in the last case (U. Oxfordian, Dorset) only one specimen is recorded.

8. INTERPRETATION OF ECOLOGY

It is clear from Section 7 that *C. (C.) virdunensis* was a highly stenotopic species, restricted to coral reef facies. As such its palaeosynecology is comparable with that of the similarly restricted species of *S. (Spondylopecten)*. Like the latter its absence from Kimmeridgian reefs at La Rochelle may relate to their dense structure (see p. 88). Failure to colonise the apparently suitable Oxfordian reefs of England may have stemmed from an intolerance of the lower temperatures of more northerly latitudes.

Recent low convexity, weakly ornamented, thin shelled morphological analogues of *C. (C.) virdunensis* include *Chlamys marshallensis*, *Ch. madreporarum* and *Ch. irregularis*, all of which live byssally attached either beneath or within coral colonies (WALLER, 1972b).

9. FUNCTIONAL MORPHOLOGY

Since *C. (C.) virdunensis* is in most morphological respects identical to *C. (C.) auritus* a similar byssate mode of life can be inferred. The maximum height of *C. (C.) virdunensis* (67.5 mm) is considerably greater than that of the morphological analogue *Ch. marshallensis* (30 mm) and this probably implies that the former did not live suspended from a byssus when adult. Large specimens probably gained additional support from contact between the disc and corals. Such support might have been obtained in crevices and the low convexity, minimally ornamented shell would have been well adapted to this microhabitat. The protection against waves and predatory attacks afforded by crevice microhabitats might be the reason behind the possession of only a thin, weak shell.

The high H/L ratio of the shell renders it probable that *C. (C.) virdunensis* could only have been a poor swimmer.

10. ORIGINS AND EVOLUTION

C. (C.) virdunensis almost certainly arose from *C. (C.) auritus*, from which it differs significantly only by the greater H/L and H/UA. Since the former ratio decreases while the latter increases during the ontogeny of *C. (C.) auritus* transspecific evolution could have been brought about by heterochrony. However, simultaneous retardation (of H/L) and acceleration (of H/UA) would have had to have taken place and it is by no means certain whether such a situation could have occurred in a single speciation event (although GOULD (1977) points out that more distantly related taxa may exhibit in the descendant, features which may be attributed to both acceleration and retardation of the ancestral ontogeny).

The limited number of measured specimens (30) precludes an exact evaluation of phyletic trends within *C. (C.) virdunensis*. However, maximum height does seem to show a genuine increase in the passage from Oxfordian (49 mm) to Kimmeridgian (60 mm) to Tithonian (67.5 mm). This, together with extreme stenotopy, is good evidence for the prevalence of 'K' selection (GOULD, 1977).

Subgenus *CAMPTOCHLAMYS* ARKELL 1930a

Type species. OD; ARKELL 1930a, p. 102; *Pecten intertextus* ROEMER 1839, p. 27, pl. 18, fig. 23; Oxfordian, N. Germany.

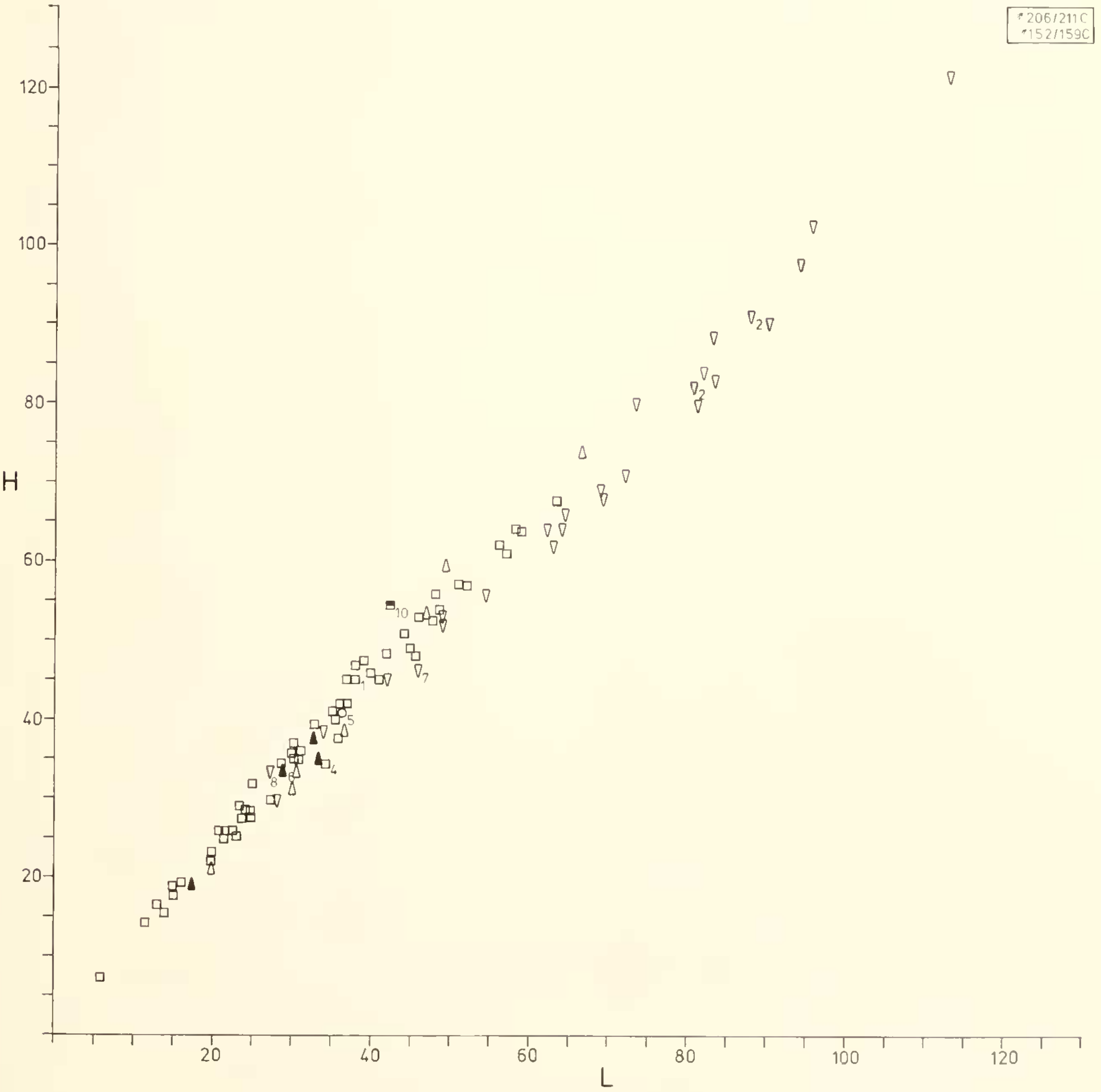
AMENDED DIAGNOSIS

Differing from *C. (Camptonectes)* in that weak radial riblets and comarginal lamellae are present giving rise to a reticulate pattern of sculpture. Jur. (Aalen.-Tithon.), ?Cret., Eur., Asia, Afr., N. Am., ?Austr.

DISCUSSION

In his diagnosis HERTLEIN (1969: N352) stated that *Camptochlamys* ranged only from the Bajocian to the 'Portlandian' (Tithonian) and was restricted to England. The stratigraphic and geographic range can now be extended to that given above. If the Cretaceous forms (see p. 136) are indeed referable to *C. (Camptochlamys)* then the subgenus *Boreionectes* ZAKHAROV 1965 should be regarded as a junior subjective synonym.

ARKELL (1930a) originally created *Camptochlamys* as a subgenus of *Chlamys*. However, COX (1952) suggested that it be transferred to *Camptonectes* because divaricate striae were seen on a specimen (BM L26669) of the type species *Pecten intertextus* ROEMER (= *C. (Cc.) clathratus* (ROEMER)). The author has been unable to trace the relevant specimen and has yet to find any further examples exhibiting divaricate ornament.



Text fig. 121: *Camptonectes (Camptochlamys) obscurus* – height/length.

The possibility of removal by abrasion cannot, however, be discounted.

Two groups may be distinguished in Jurassic *C. (Camptochlamys)* on the following basis:

1. Radial striae reaching the ventral margin at all stages in ontogeny (= *C. (Cc.) clathratus*).
2. Radial striae restricted to within a few cm. of the umbo (= *C. (Cc.) obscurus*).

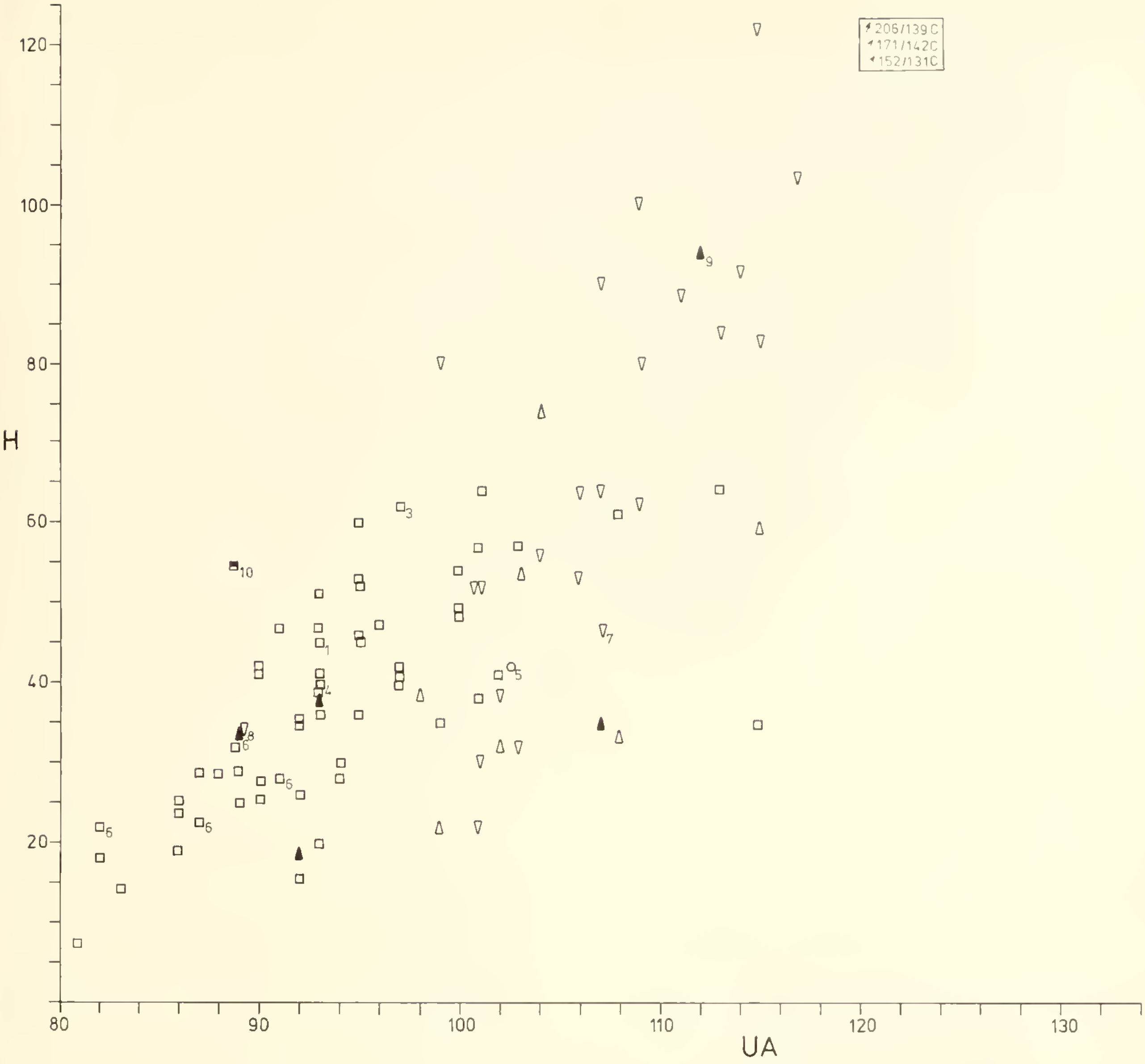
Camptonectes (Camptochlamys) obscurus (J. SOWERBY 1818)

Pl. 4, Figs. 17–22, 24, 25; text figs. 121–130

Synonymy

v* 1818 *Pecten obscura* sp. nov; J. SOWERBY, p. 3, pl. 205, fig. 1.
v* 1819 *Pecten lamellosus* sp. nov; J. SOWERBY, p. 67, pl. 239.
v* 1826a *Pecten annulatus* sp. nov; J. DE C. SOWERBY, p. 80, pl. 542, fig. 1.
1833 *Pecten obscurus* J. SOWERBY; GOLDFUSS, p. 48, pl. 91, fig. 1.
1833 *Pecten annulatus* J. DE C. SOWERBY; GOLDFUSS, p. 49, pl. 91, fig. 2.
1836 *Pecten sublaevis* sp. nov; ROEMER, p. 70, pl. 3, fig. 16.
1837 *Pecten concinnus* sp. nov; KOCH and DUNKER, p. 42, pl. 5, figs. 4a, 4b.
? 1837 *Pecten concentricus* sp. nov; KOCH and DUNKER, p. 43, pl. 5, fig. 8.
1850 *Pecten Germaniae* sp. nov; D'ORBIGNY, v. 1, p. 314.
1850 *Pecten Obrinus* sp. nov; D'ORBIGNY, v. 1, p. 373 (BOULE, 1927, v. 16, p. 131, 1928, v. 17, pl. 6, figs. 5, 6).
1852 *Pecten circinalis* sp. nov; BUVIGNIER, p. 24, pl. 19, figs. 13–15.
1853 *Pecten annulatus* J. DE C. SOWERBY; MORRIS and LYCETT, p. 12, pl. 1, fig. 13.
1853 *Pecten Germaniae* D'ORBIGNY; CHAPUIS and DEWALQUE, p. 214, pl. 29, fig. 2.
v 1858 *Pecten lens* J. SOWERBY; QUENSTEDT, p. 432, pl. 59, fig. 3 (non pl. 59, fig. 4, non p. 322, pl. 44, fig. 12, p. 354, pl. 46, fig. 20, pl. 48, fig. 8; non J. SOWERBY sp.).
? 1859 *Pecten Grenieri* sp. nov; CONTEJEAN, p. 311, pl. 23, figs. 7–9.
? 1859 *Pecten Flamandi* sp. nov; CONTEJEAN, p. 312, pl. 24, figs. 1, 2.
1860 *Pecten lamellosus* J. SOWERBY; COQUAND, p. 91.
1861 *Pecten annulatus* J. DE C. SOWERBY; TRAUTSCHOLD, p. 446.
non 1862 *Pecten flamandi* CONTEJEAN; THURMANN and ÉTALLON, p. 264, pl. 37, fig. 1.
? 1862 *Pecten Greneieri* CONTEJEAN; THURMANN and ÉTALLON, p. 265, pl. 37, fig. 7.
1864 *Pecten sublaevis* ROEMER; V. SEEBACH, p. 100.
(?) 1864 *Pecten concentricus* KOCH and DUNKER; V. SEEBACH, p. 100.
1866 *Pecten lamellosus* J. SOWERBY; DE LORIOL and PELLAT, p. 103, pl. 10, fig. 4.
1869 *Pecten exaratus* sp. nov; TERQUEM and JOURDY, p. 128, pl. 13, fig. 17.
non 1872 *Pecten Grenieri* CONTEJEAN; DE LORIOL et al., p. 382, pl. 22, figs. 5, 6.
? 1875 *Pecten Flamandi* CONTEJEAN; DE LORIOL and PELLAT, p. 194, pl. 22, figs. 6, 7.
v? 1883 *Pecten* aff. *Grenieri* CONTEJEAN; BOEHM, p. 603, pl. 67, figs. 17, 18.
? 1883 *Pecten lens* J. SOWERBY; LAHUSEN, p. 23, pl. 2, fig. 1.
1888 *Pecten subannulatus* sp. nov; SCHLIPPE, p. 128, pl. 2, fig. 3.
(?) 1891 *Pecten concentricus* KOCH and DUNKER; BEHRENDSEN, p. 416.
non 1893 *Pecten (Camptonectes)* cf. *Grenieri* CONTEJEAN; FIEBELKORN, p. 399, pl. 14, fig. 11.
? 1894 *Pecten chavattensis* sp. nov; DE LORIOL, p. 55, pl. 6, fig. 8.
1910 *Pecten (Camptonectes) Broenlundi* sp. nov; RAVN, p. 465, pl. 34, figs. 5, 6.
1917 *Pecten annulatus* J. DE C. SOWERBY; BORISSIAK and IVANOFF, p. 25, pl. 1, fig. 14.
1925 *Pecten* cf. *annulatus* J. DE C. SOWERBY; STEFANINI, p. 161, pl. 29, fig. 1.
v 1926 *Camptonectes lens* var. *annulatus* (J. DE C. SOWERBY); STAESCHE, p. 79, pl. 3, fig. 12.
1926 *Camptonectes Sowerbyi* sp. nov; STAESCHE, p. 81, pl. 3, fig. 7.
? 1931 *Pecten (Camptonectes)* cf. *lens* J. SOWERBY; SOKOLOV and BODYLEVSKY, p. 55, pl. 4, fig. 7.
1934 *Pecten (Camptonectes) lens* var. *annulatus* J. DE C. SOWERBY; STOLL, p. 22.
1935a *Camptonectes browni* sp. nov; COX, p. 177, pl. 18, figs. 13a, 13b.
1935 *Camptonectes lamellosus* (J. SOWERBY); SALIN, p. 140.
? 1936 *Camptonectes praecinctus* sp. nov; SPATH, p. 104, pl. 40, fig. 6, pl. 41, fig. 1.
1936 *Camptonectes lens* var. *exaratus* (TERQUEM and JOURDY); DECHASEAUX, p. 30.
1936 *Camptonectes annulatus* (J. DE C. SOWERBY); DECHASEAUX, p. 31, pl. 4, fig. 10.
v* 1936 *Camptonectes Richei* sp. nov; DECHASEAUX, p. 32, pl. 4, figs. 12–15, pl. 5, figs. 1, 2.
1936 *Camptonectes Sowerbyi* STAESCHE; DECHASEAUX, p. 33.
non 1936 *Camptonectes Flamandi* (CONTEJEAN); DECHASEAUX, p. 35.
1936 *Camptonectes circinalis* (BUVIGNIER); DECHASEAUX, p. 36.
1936 *Camptonectes lamellosus* (J. SOWERBY); DECHASEAUX, p. 36, pl. 5, fig. 11.
v non 1936 *Aequipecten Greneri* (CONTEJEAN); DECHASEAUX, p. 52, pl. 8, fig. 7.
1939 *Camptonectes Germaniae* (D'ORBIGNY); STEFANINI, p. 171, pl. 19, fig. 11.
1948 *Camptonectes annulatus* (J. DE C. SOWERBY); COX and ARKELL, p. 13.
1948 *Camptonectes (Camptochlamys) obscurus* (J. SOWERBY); COX and ARKELL, p. 14.
v* 1952 *Camptonectes indicus* sp. nov; COX, p. 25, pl. 3, figs. 1–4.
? *1961* *Camptonectes* aff. *browni* COX; HAYAMI, p. 67.
1961 *Camptonectes annulatus* (J. DE C. SOWERBY); ROSSI RONCHETTI and FANTINI SESTINI, p. 121, pl. 13, fig. 10.
? 1974 *Camptonectes waggrakinensis* sp. nov; SKWARKO, p. 82, pl. 25, figs. 1, 4.
p 1978 *Camptonectes laminatus* (J. SOWERBY); BRADSHAW, p. 313 (non J. SOWERBY sp.).
1978 *Camptonectes (Camptochlamys) obscurus* (J. SOWERBY); BRADSHAW, p. 314.
1979 *Camptonectes annulatus* (J. DE C. SOWERBY); T. PALMER, p. 196.

Holotype (M) of *Pecten obscura* J. SOWERBY 1818, p. 3, pl. 205, fig. 1; BM 43325; Pl. 4, Fig. 24 herein; H: 45, L: 38, HAA: 8.5, AH: 15, N: 5.5, UA: 93; Stonesfield Slate (L. Bathonian), Stonesfield, Oxfordshire.



Text fig. 122: *Camptonectes (Camptochlamys) obscurus* – height/umbonal angle.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

'Spec. Char. Sub-orbicular, depressed, with obscure arched longitudinal rugae upon the surface; ears large.

Somewhat longer than wide: the surface is dull, almost smooth; but it has some indications of diverging furrows. The edge is thick.

Occurs upon the sandy Limestone slate of Stonesfield, near Oxford. My specimen was forwarded to me long since by Dr. WILLIAMS.'

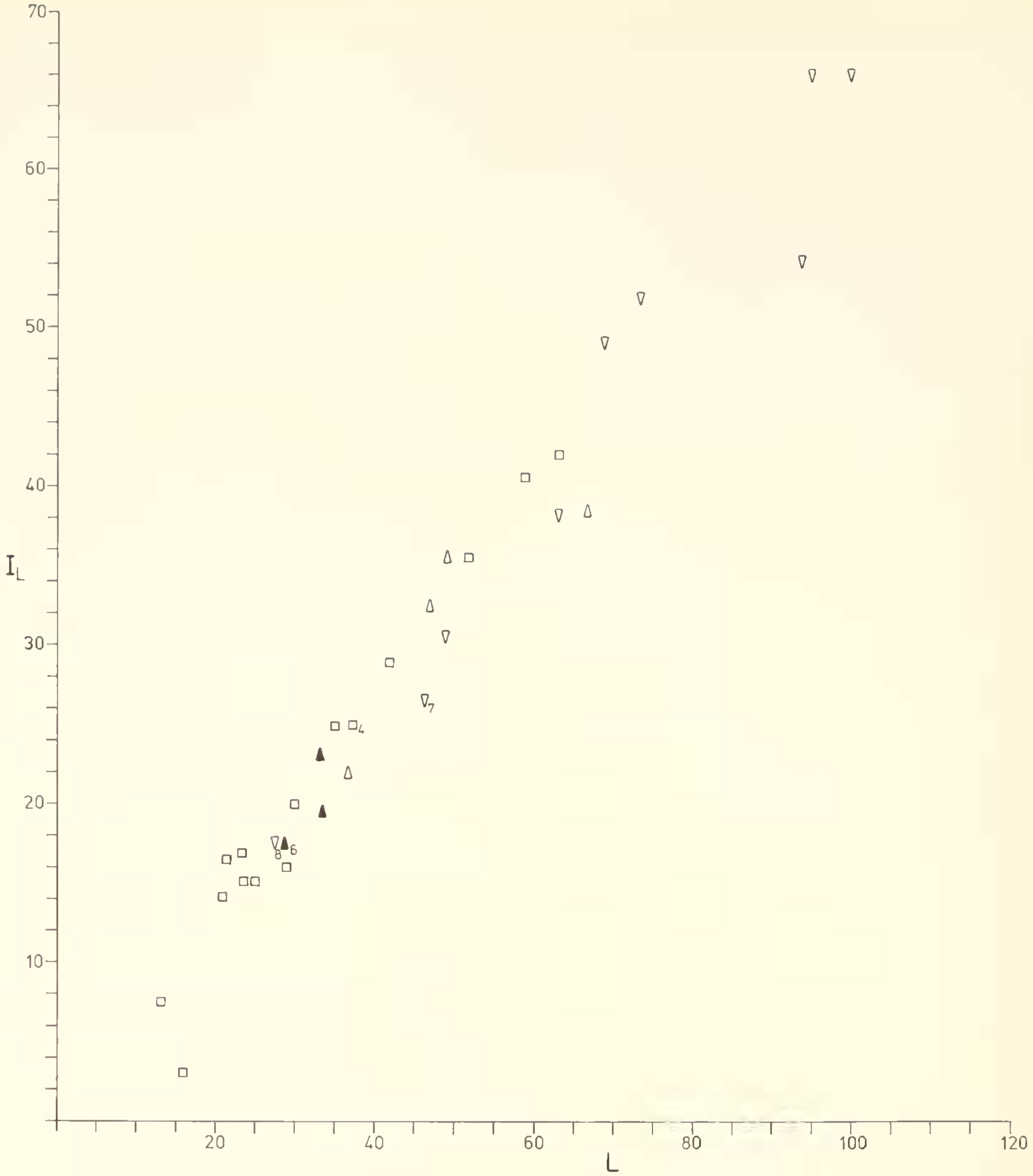
2. AMENDED DIAGNOSIS

Distinguished from *C. (Camptochlamys) clathratus* by the fact that the radial striae extend no more than a few centimetres from the umbo and are thereafter replaced by divaricate striae.

3. AMENDED DESCRIPTION

Essentially similar to *C. (Camptonectes) auritus*. Differing by the presence of comarginal lamellae and radial striae (Pl. 4, Fig. 22) of variable length, greater maximum height (122 mm, OUM J37483; ?206 mm, see Section 7), higher mean H/UA (text fig. 122), greater convexity of the left valve, isometric increase in anterior hinge length and right valve intersinal distance to give higher values of AH/L (text fig. 127) and I_R/L (text fig. 124) late in ontogeny, isometric increase of anterior auricle height to give lower values of HAA/L (text fig. 126) late in ontogeny and allometric increase of posterior hinge length to give higher values of PH/L (text fig. 128) late in ontogeny. The remaining metric characters are plotted in text figs. 121, 123, 125.

Unlike *C. (C.) auritus* there appear to be no phyletic changes in metric proportions beyond an increase in size and a possible accentuation of allometric decrease in H/L in Tithonian as compared to Bathonian individuals.



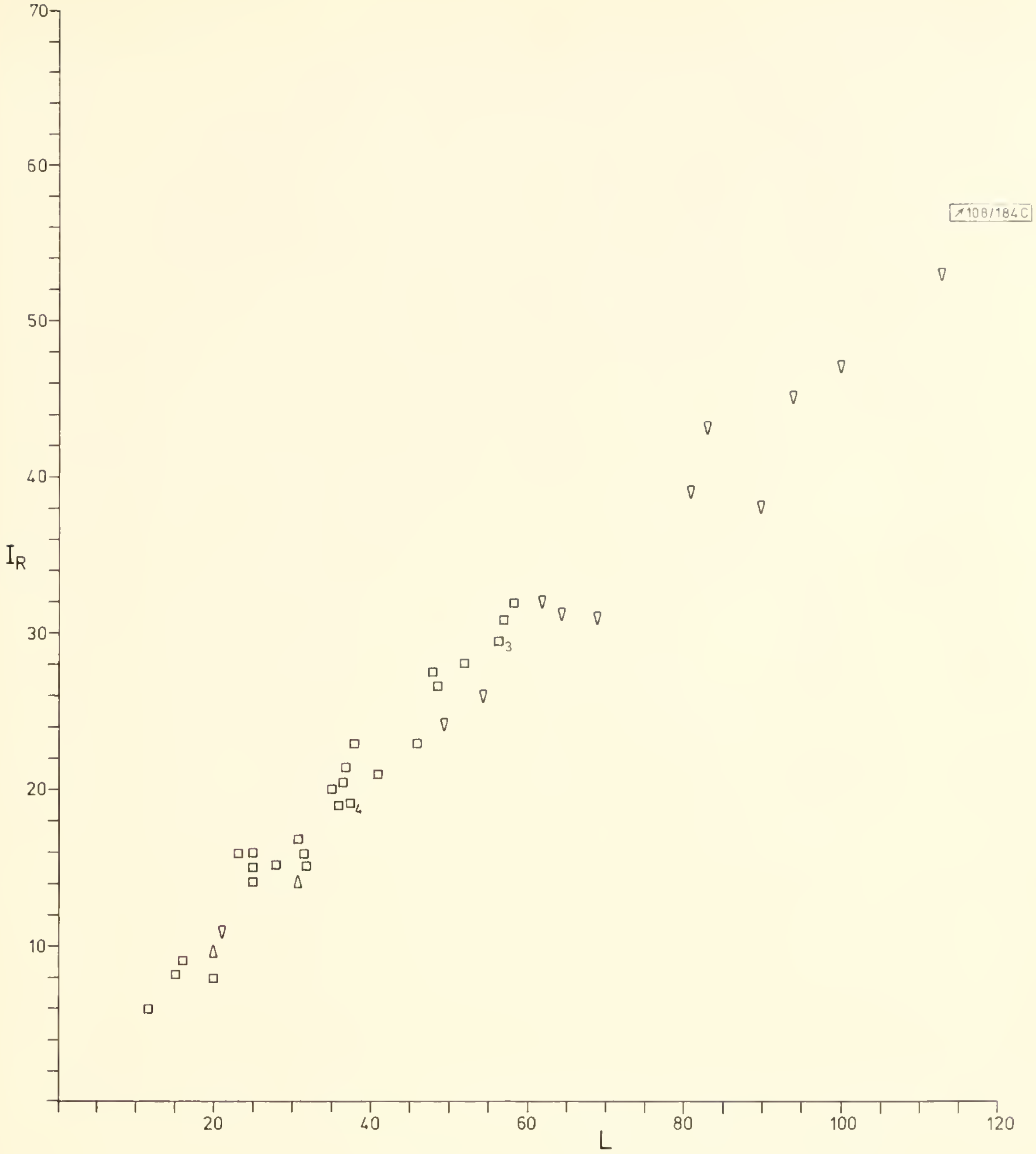
Text fig. 123: *Camptonectes (Camptochlamys) obscurus* – intersinal distance on left valve/length.

4. DISCUSSION

A disjunct stratigraphic distribution with two distinct peaks in abundance (see Sections 5, 7) has resulted in the evolution of two taxonomic schemes (centred on species erected by the Sowerbys for Bathonian and Tithonian examples) for M. and U. Jurassic representatives of the species described in Section 3. There is, however, no biological basis for maintaining a distinction and in the absence of any evidence for the existence of separate lineages such differences as exist between earlier and later populations (see Section 3) can be most parsimoniously explained in terms of phyletic evolution (see Section 10). Large L. Cretaceous forms (usually referred to *Camptonectes cinctus* J. Sowerby) are probably also phyletic descendants but their systematics are excluded from this discussion because the present author has yet to survey the literature and has examined relatively few specimens. Suffice it to say that metric proportions (c) would plot within the range of Jurassic ontogenies if these were projected to larger sizes.

The following types and figures of types from the Jurassic are inseparable from the species described in Section 3 on the basis of metric proportions:

1. The holotype (M) of *'Pecten' obscura* J. Sowerby (BM 43325; Pl. 4, Fig. 24).
2. Two syntypes of *'P.' lamellosus* J. Sowerby (BM 43299; Pl. 4, Fig. 17).
3. The holotype (M) of *'P.' annulatus* J. de C. Sowerby (BM 43301; Pl. 4, Fig. 18).

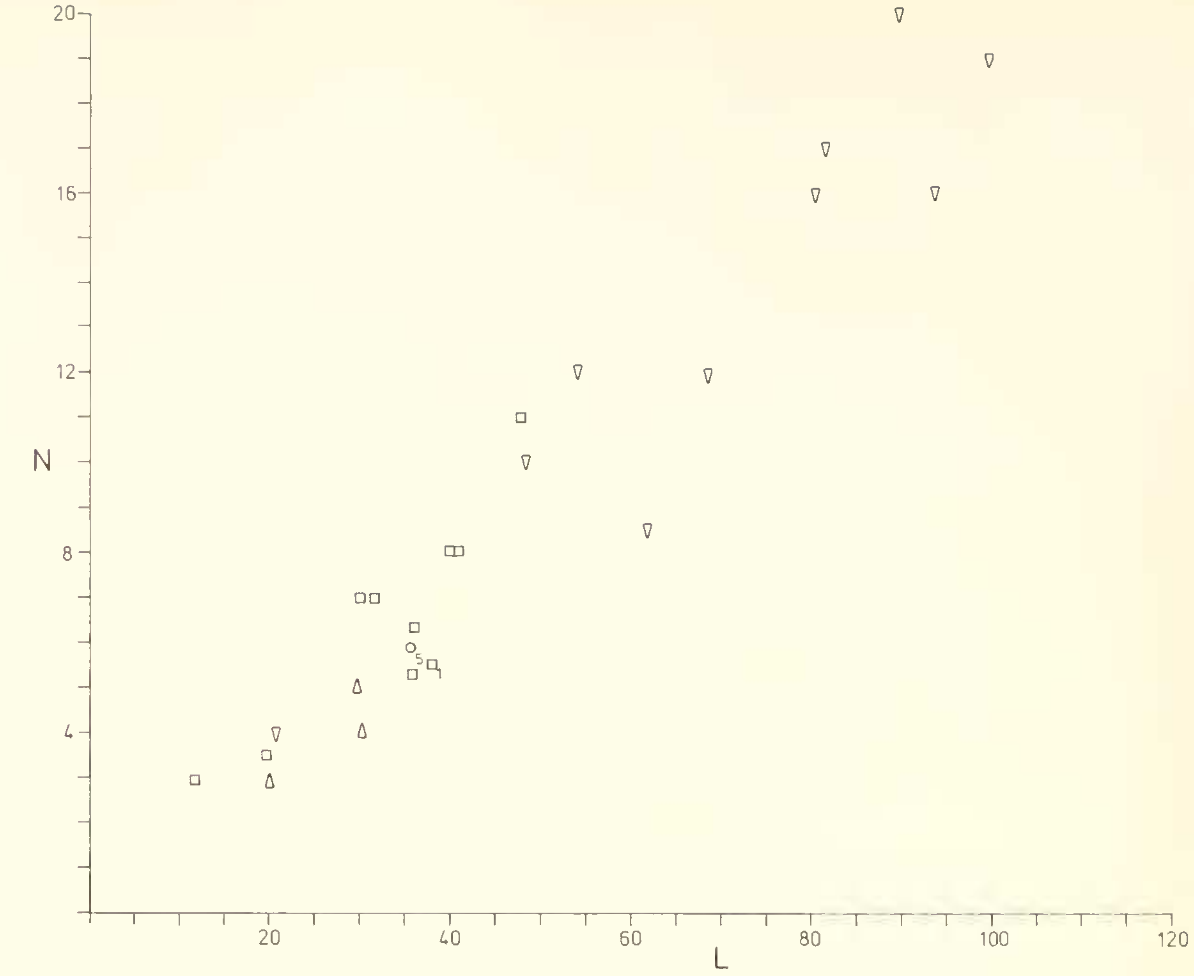


Text fig. 124: *Camptonectes (Camptochlamys) obscurus* – intersinal distance on right valve/length.

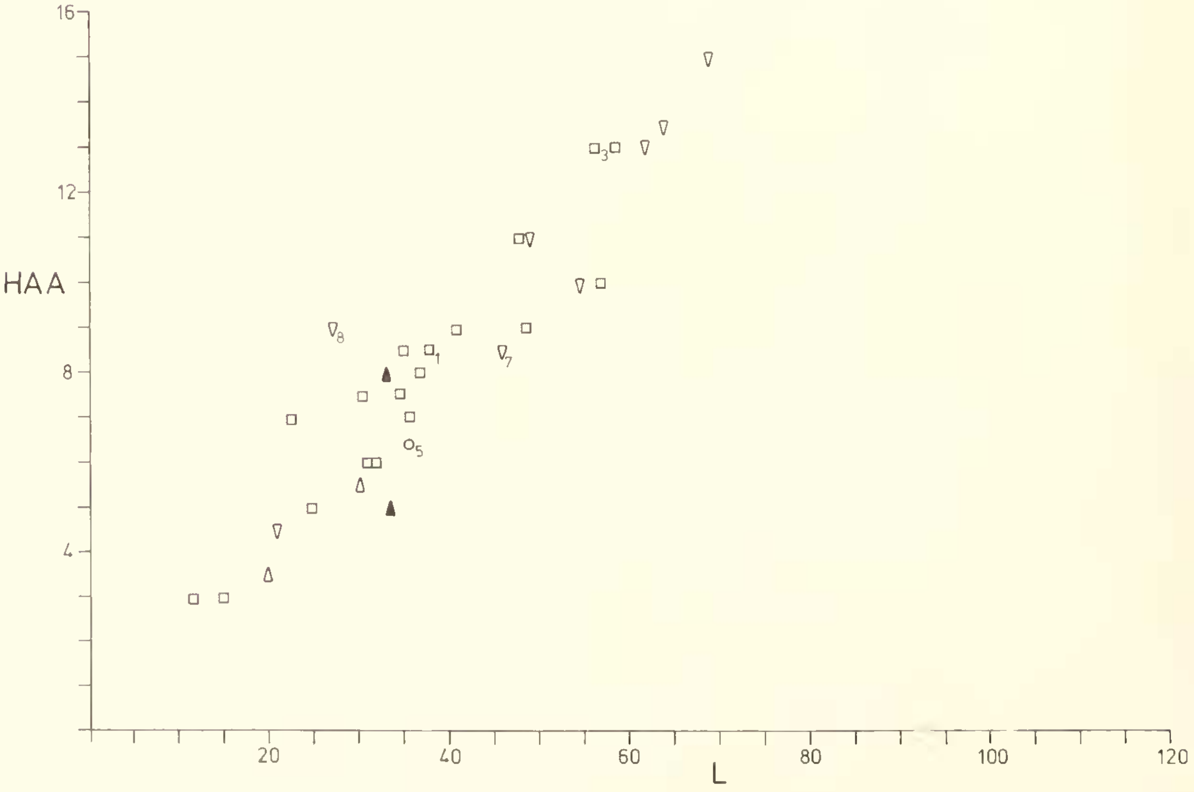
4. The sole observed type of *'P.' exaratus* Terquem and Jourdy (ENSM L335).
5. A paratype of *Camptonectes indicus* Cox (BM L75265; Pl. 4, Fig. 25).
6. The type series of *C. Richei* Dechaseaux (NM).
7. The original figure of *'P.' sublaevis* Roemer.
8. The original figure of *'P.' concinnus* Koch and Dunker.
9. The original figure of *C. Sowerbyi* Staesche.

In none of the foregoing cases does any difference in ornament provide a basis for distinction. The subdued ornamentation of *'P.' obscura*, *'P.' exaratus* and *C. Richei* is clearly the result of wear. Varietal use of *'P.' annulatus* in Staesche (1926) and Stoll (1934) and of *'P.' exaratus* in Dechaseaux (1936) does not depart from the original authors' hypodigms. *'P.' sublaevis* Roemer should be permanently rejected since it is a junior primary homonym of *'P.' sublaevis* Young and Bird (itself a junior subjective synonym of *Pseudopecten (Ps.) equivalvis)*.

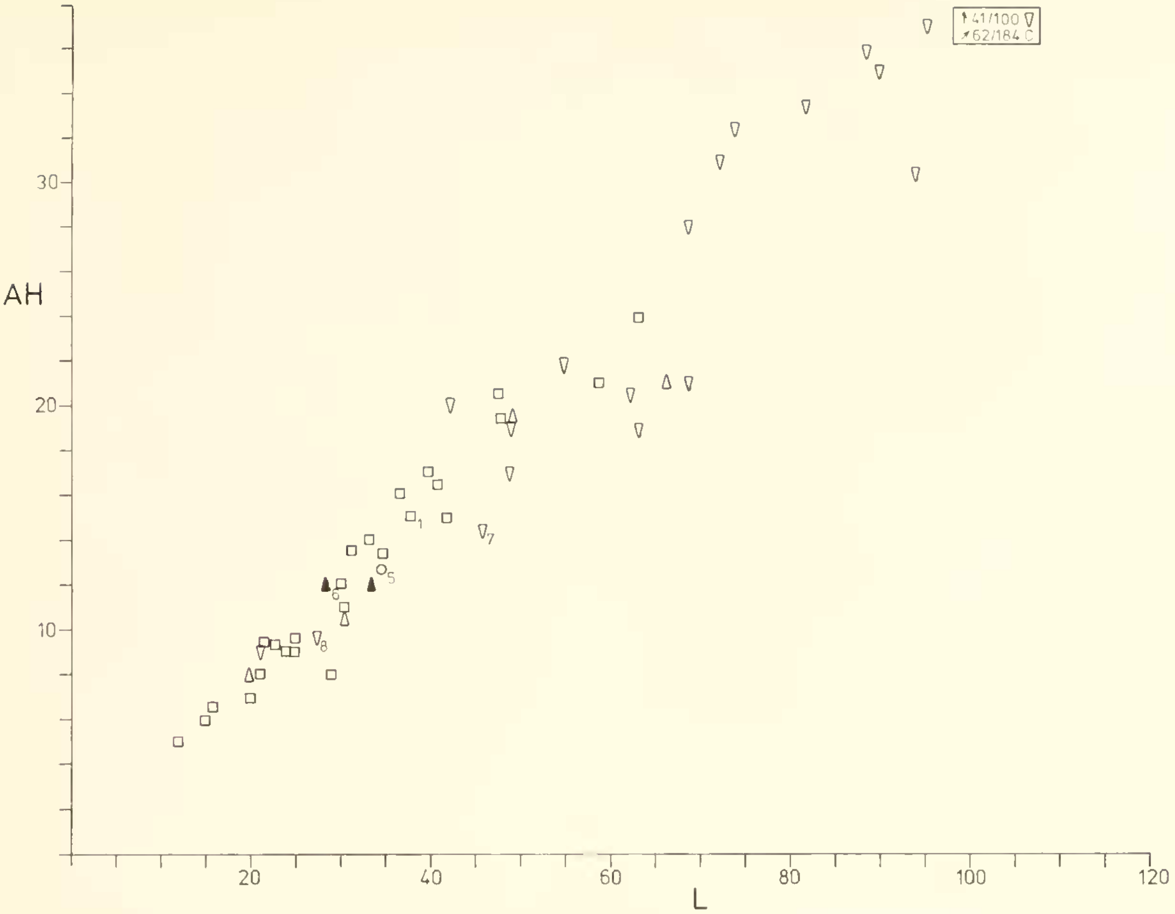
Figures of the types of *'P.' Obrinus* d'Orbigny, *P. circinalis* Buvignier, *'P.' subannulatus* Schlippe, *'P.' Broenlundi* Ravn and *C. browni* Cox were not measured but in each case the ornament does not differ significantly from that of the species described in Section 3. Hayami's (1961) record of a specimen resembling Cox's species must be treated sceptically in view of the disjunct geographic position (Japan) and lack of a figure. Although a figure is provided of *C. waggrakinensis* Skwarko (from W. Australia) the original is very poorly preserved. Nevertheless comparison with *'P.' cinctus* J. Sowerby suggests that it could be synonymous with the



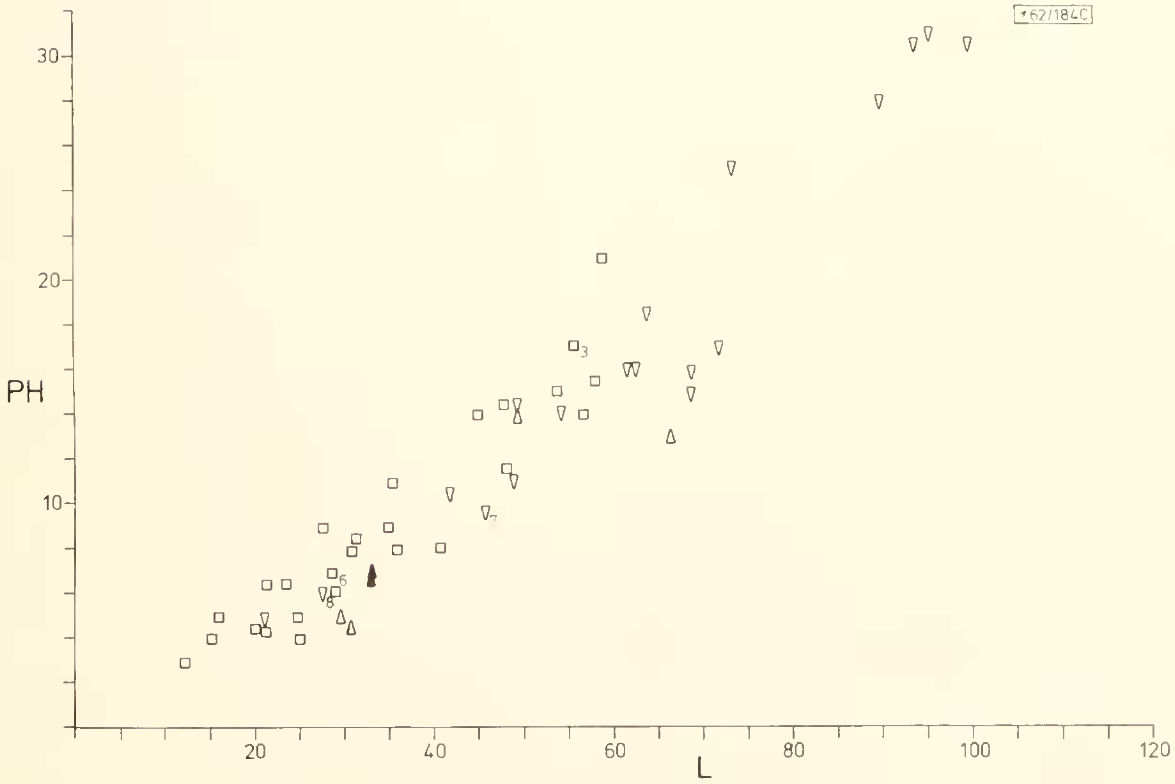
Text fig. 125: *Camptonectes (Camptochlamys) obscurus* – depth of byssal notch/length.



Text fig. 126: *Camptonectes (Camptochlamys) obscurus* – height of anterior auricle/length.



Text fig. 127: *Camptonectes (Camptochlamys) obscurus* – anterior hinge length/length.



Text fig. 128: *Camptonectes (Camptochlamys) obscurus* – posterior hinge length/length.

species described in Section 3 (see above). The figure of *'P.' chavattensis* de Loriol depicts a specimen with reticulate ornament, as is characteristic of *C. (Camptochlamys)*, and mention in the description of 'punctae' on the right valve suggests that it may be referable to the species described in Section 3.

'P.' Germaniae d'Orbigny was erected for a specimen from the Kimmeridgian assigned to *'P.' annulatus* J. de C. Sowerby by Goldfuss (1833). Presumably d'Orbigny (1850) considered that the horizon of derivation merited a distinction from J. de C. Sowerby's species, whose holotype is from the Bathonian. However, the present author's inclusion of both M. and U. Jurassic specimens within the same hypodigm renders this insufficient grounds for a specific separation.

The original figure of *'P.' concentricus* Koch and Dunker appears to depict the comarginally ornamented right valve of *Entolium (E.) orbiculare* but the fact that v. Seebach (1864) and Behrendsen (1891), both of whom may have examined the type material, have applied the specific name to specimens with radial as well as comarginal ornament suggests that it may be a reversed illustration of the left valve of the species described in Section 3. Although H/L and H/UA (10) are both high for the latter species they are considerably less distant than from *E. (E.) orbiculare*.

Although one of the original figures (pl. 40, fig. 6) of *C. praecinctus* Spath (Tithonian) has metric proportions (H: 168, L: 165, UA: 128) within the range of projected ontogenies of the species described in Section 3, the other (pl. 41, fig. 1) has a rather low H/UA (100/40), which, together with the poor development of comarginal lamellae, suggests that the species may in fact be synonymous with *C. (C.) auritus*.

The affinities of Contejean's (1859) species *'P.' Grenieri* and *'P.' Flamandi* and secondary references thereto are dealt with under *Radulopecten strictus* and *C. (C.) virdunensis* respectively.

The original (GPIT) of *'P.'lens* J. Sowerby; Quenstedt (1858, pl. 59, fig. 3 only) has radial striae in the umbonal region and is clearly referable to the species described in Section 3 rather than Sowerby's species (= *C. (C.) auritus*). Records of J. Sowerby's species in Lahusen (1883) and Sokolov and Bodylevsky (1931) are discussed under *C. (C.) auritus*. Specimens said to have strong comarginal ornament but which were referred to *C. laminatus* by Bradshaw (1978) are probably representative of the species described in Section 3.

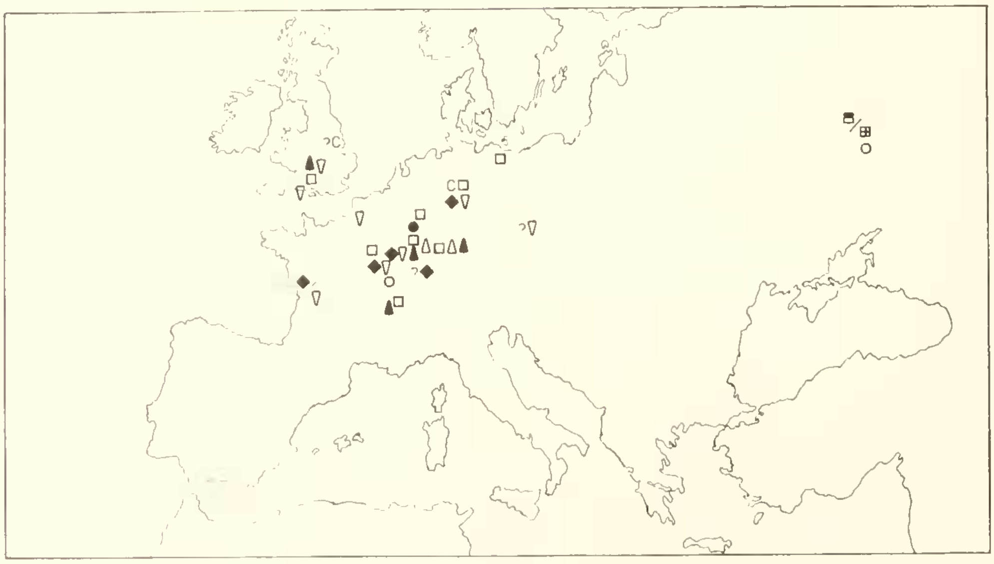
Of the synonymous species discussed above the earliest available name for the species described in Section 3 is *'P.' obscura* J. Sowerby.

5. STRATIGRAPHIC RANGE

The first records of *C. (Cc.) obscurus* are from the Aalenian (Murchisonae zone) of Swabia (Staesche, 1926). A few specimens are recorded from the Bajocian of S. Germany (Quenstedt, 1858), E. France (Dechaseaux, 1936) and the Cotswolds (BM 73397, L5125, L17573, L41949, L84344, L95180, LL24287) but the species does not become common until the Bathonian. Callovian records from Europe are limited to Lahusen (1883) and a few specimens in DM while Oxfordian records are limited to Buvignier (1852). Definite records from the Kimmeridgian are restricted to Goldfuss (1833), Koch and Dunker (1837), v. Seebach (1864) and Dechaseaux (1936). However, the species becomes common again in the Tithonian and if specimens such as BM L1354 and L24189 are included within *C. (Cc.) obscurus* (see Section 4) the stratigraphic range can be said to extend into the L. Cretaceous at least as far as the Hauterivian.

6. GEOGRAPHIC RANGE

C. (Cc.) obscurus was essentially a Boreal species. Thus for most of its stratigraphic range distribution was centred in N. Europe (text fig. 129) and in the later (Tithonian-L. Cretaceous) parts of its stratigraphic range the centre of distribution shifted outside continental Europe, into Britain (see Section 7).



Text fig. 129: *Camptonectes (Camptochlamys) obscurus* – European distribution.

Text fig. 130: *Camptonectes (Camptochlamys) obscurus* – World distribution (Callovian reconstruction).

The paucity of Callovian records in Europe (see Section 5) is probably the result of the widespread development of unfavourable clay facies (see Section 8). Records from the Callovian of Somalia (Cox, 1935a) and India (Cox, 1952) and ?Callovian of Afghanistan (Rossi Ronchetti and Fantini Sestini, 1961) may thus signify migration to more suitable environments (text fig. 130). Similarly the rarity of the species in the Bajocian and Oxfordian of Europe may correlate with occurrences in the Bajocian of Somalia (Stefanini, 1939) and possible occurrences in the Bajocian (Skwarko, 1974) and Oxfordian (a poorly preserved, unlocalised and unnumbered specimen in the BM) of Australia. However, in these cases exclusion from Europe was more probably the result of competition with *C. (C.) auritus* since suitable sedimentary environments were widespread (see Section 8).

7. DESCRIPTION OF ECOLOGY

In the Aalenian of Swabia *C. (Cc.) obscurus* occurs in chamosite oolites in association with common examples of *Propeamussium (P.) pumilum* and *Entolium (E.) corneolum*. The maximum height attained is 74 mm (GPIT). *C. (C.) auritus* is a fairly rare associate but in similar almost contemporaneous sediments in central England (Northampton Sand Ironstone) it is common while *C. (Cc.) obscurus* is unknown. *C. (C.) auritus* is also common throughout the Bajocian in Europe but *C. (Cc.) obscurus* is generally rare (see Section 5). However an isolated specimen (Staesche, 1926) attains a maximum height of 93.8 mm.

In the Bathonian of Britain *C. (Cc.) obscurus* is particularly common in the Stonesfield Slate (L. Bathonian) where the most common faunal associates are oysters and '*Trigonia impressa*' together with rhynchonellid brachiopods and cidaroid echinoids. The sediments are flat laminated calcareous sandstones and sandy oolites. The species also occurs, albeit somewhat less commonly, in grain supported shelly oolites of roughly the same age at Minchinhampton and in the U. Bathonian Forest Marble. In both cases *C. (C.) laminatus* is a fairly common associate and at the former locality *C. (Cc.) clathratus* also occurs quite frequently. The sedimentary and faunal associations of most other Bathonian occurrences of *C. (Cc.) obscurus* are unclear. However in the M./U. Bathonian White Limestone Formation of the Cotswolds the species occurs in muddy lime sands,where the principal faunal associates are *Praeexogyra hebridica* and *Isognomon isognomoides*, and in shelly micrites where the brachiopod *Epithyris* is the dominant faunal element. *C. (Cc.) obscurus* is absent from lime sands and pelleted lime muds in the same formation (T. Palmer, 1979) but it may occur in sands and oyster reefs further northeast in the Rutland Formation (Bradshaw, 1978, see Section 4). The maximum height attained by the species in the Bathonian is 69 mm (BM L10962).

C. (Cc.) obscurus is rare in the Callovian of W. Europe (see Section 5), where the stage is widely developed in clay facies, but is known from a limestone sequence containing chamosite oolite beds in Russia (Lahusen, 1883). Oolitic deposits are widespread in the Oxfordian of Europe but *C. (Cc.) obscurus* is absent from them, the only record of the species in the Oxfordian being from marls (Buvignier, 1852). *C. (C.) auritus* and *C. (C.) clathratus* are however quite common in Oxfordian oolites as well as other sediments.

C. (Cc.) obscurus is rare in the L. Kimmeridge Clay (Kimmeridgian) but is occasionally found in the sandy marginal facies developed in the upper part of the formation (M. Tithonian) in S. England and N. W. France. *C. (C.) auritus* is much more common at the latter horizon but in the U. Tithonian it is rare and *C. (Cc.) obscurus* is common, reaching a maximum height of 122 mm (OUM J37483). In Dorset *C. (Cc.) obscurus* occurs most abundantly at three levels in the U. Tithonian; within the Portland Sand Formation,in the *Exogyra* Beds (Corton Hill Member),and within the Portland Stone Formation,in the Basal Shell Bed (Dungy Head Member) and the Freestone Series (Winspit Member). In each case there is a diverse associated ammonite, gastropod and bivalve fauna including the genera *Trigonia*, *Protocardia*, *Isognomon*, *Pleuromya* and *Exogyra*. Records from Tithonian marls and limestones (Calcaire de Barrois) in the E. Paris Basin (Salin, 1935) are associated with a much less diverse fauna (lacking in ammonites and dominated by '*Corbula*', '*Leptoxis*', '*Lioplax*' and '*Melania*') and specimens from the 'Kimmeridgian/Portlandian' (KOCH and DUNKER, 1837) and 'L. and U. Kimmeridge' (v. SEEBACH, 1864) of L. Saxony are probably derived from horizons with a similarly restricted fauna (HOLDER, 1964; HUCKRIEDE, 1967).

Specimens usually referred to *C. cinctus* J. SOWERBY but which are likely to be phyletic descendants of *C. (Cc.) obscurus* (see Section 4) are found in the Valanginian and Hauterivian of Lincolnshire, where they reach a maximum height of 206 mm (BM L1354). The horizons of greatest abundance appear to be the Claxby Ironstone (a chamosite oolite containing a diverse fauna including the bivalves *Exogyra*, *Trigonia* and *Cucullaea* together with ammonites and belemnites) and the Tealby Limestone (a sequence of sandy limestones, clays and shales). A single specimen (BM L24189) is known from roughly contemporaneous deposits in N. Germany but there are no records from further south in Europe.

8. INTERPRETATION OF ECOLOGY

The oolitic limestones and ironstones most commonly occupied by *C. (Cc.) obscurus* are indicative of generally high energy levels and SELLWOOD and MCKERROW (1974) have suggested that periodic storms were an important factor during the deposition of the Stonesfield Slate, in which the species is particularly common. The levels at which *C. (Cc.) obscurus* is most abundant in the U. Tithonian of Dorset are indicative of regression (TOWNSON, 1975) and one can assume that shallowing of the sea resulted in higher environmental energy from the increased effect of waves and currents.

The rarity of *C. (Cc.) obscurus* in most argillaceous sequences suggests that the species could not tolerate low energy environments. However, evidence from the White Limestone Formation, where low energy environments were apparently preferentially colonised, belies this reasoning and suggests moreover that the abundance of the species in oolitic limestones, ironstones etc. is not due to a particular liking for high energy environments. A dependence on the pre-existence of some specific element of the fauna (perhaps oysters) for the provision of byssal attachment sites for the juvenile (see Section 9) may have been the primary determinant of distribution.

The occurrence of *C. (Cc.) obscurus* in the Calcaire de Barrois is evidence, according to the facies interpretation of SALIN (1935), of a tolerance of reduced salinities. The occurrence of the species in the Kimmeridgian/Tithonian sequence of L. Saxony provides further evidence of a tolerance of reduced salinities if the facies interpretation of HUCKRIEDE (1967) is followed but is evidence of an additional tolerance of high salinities if the facies interpretation of JORDAN (1971) is adopted. If confirmed, records from the Bathonian of the E. Midlands would be evidence of a tolerance of fluctuating as well as low salinities (see. p. 129).

There is a very noticeable inverse correlation between the numbers of *C. (Cc.) obscurus* and *C. (C.) auritus* at any one time or place which is strongly suggestive of competition. There is however little evidence of a similar reaction between *C. (Cc.) obscurus* and *C. (C.) laminatus* and although the rarity of *C. (Cc.) obscurus* in the Oxfordian is matched by a corresponding abundance of *C. (Cc.) clathratus* competition can hardly be invoked in explanation because the species occur together in numbers in the Bathonian. The rarity of *C. (Cc.) obscurus* in the Oxfordian is more probably the result of competitive exclusion by *C. (C.) auritus* which occurs widely in the stage.

9. FUNCTIONAL MORPHOLOGY

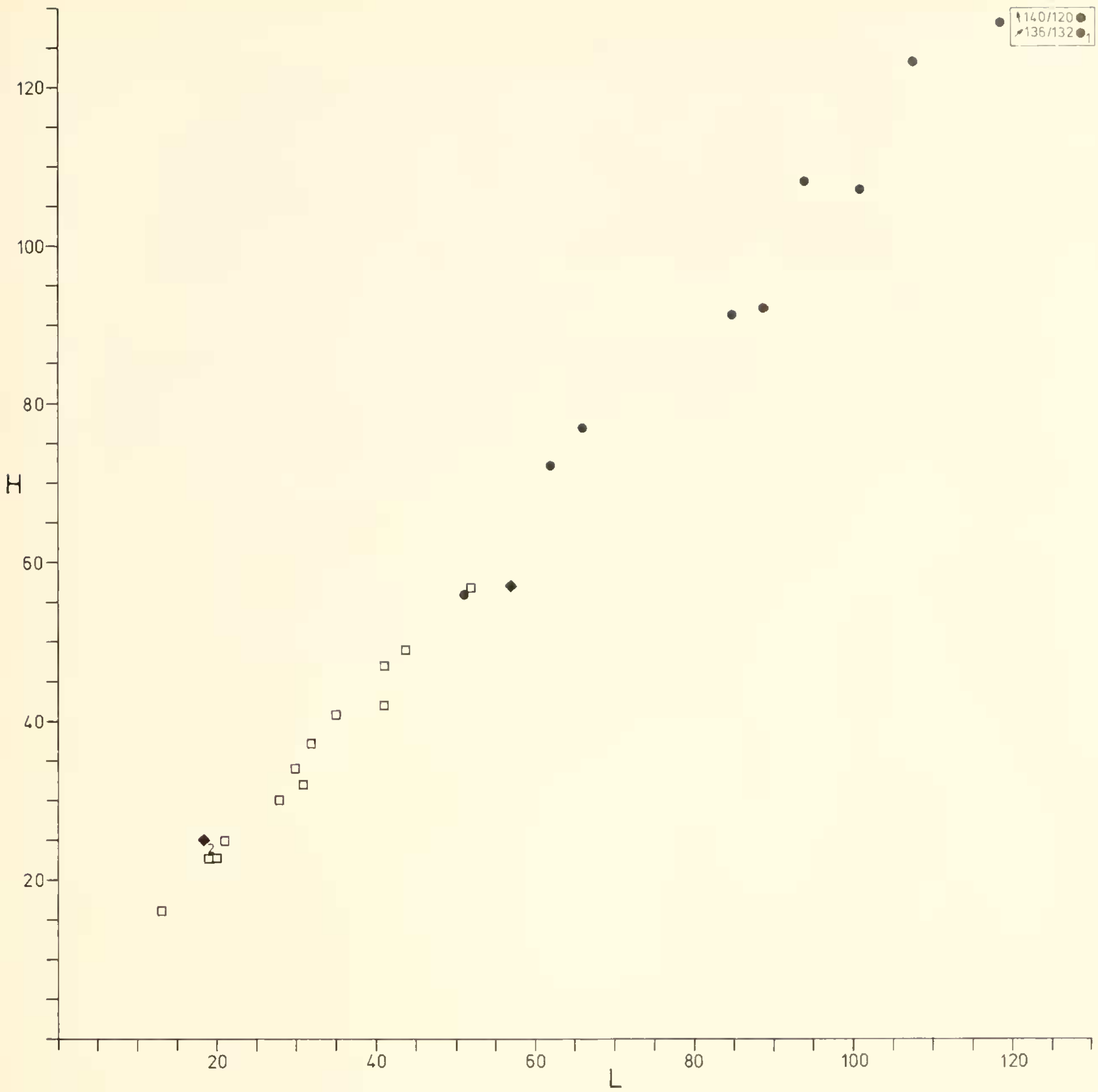
Since *C. (Cc.) obscurus* is comparable to *C. (C.) auritus* in most aspects of morphology, a similar juvenile byssate followed by adult reclining mode of life can be inferred. The greater shell thickness and H/UA of *C. (Cc.) obscurus* probably led to the loss of swimming ability at an earlier age, although some compensation may have been derived from the greater convexity of the left valve. In spite of an apparent phyletic reduction in H/L it is still very doubtful whether adult representatives of later populations could have swum.

STAESCHE (1926) considered the strong comarginal lamellae on the disc to be an adaptation for stability in high energy environments. However, in view of the fact that lamellae are usually more strongly developed on the left valve (not in contact with the substrate) and that the non-lamellate species *C. (C.) laminatus* occurs with *C. (Cc.) obscurus* in high energy environments, STAESCHE's hypothesis is implausible. A more likely explanation is that the lamellae provided camouflage or, as STAESCHE also hypothesised, that they served to strengthen and stiffen the shell against predatory attacks, to which the animal must have been susceptible in the sessile adult stage.

10. ORIGINS AND EVOLUTION

C. (Cc.) obscurus almost certainly arose from *C. (C.) auritus*. Regulatory gene evolution leading to heterochrony can be invoked to explain differences in UA, HAA and AH. However, simultaneous acceleration (for the first two) and retardation (for the last) would have to have occurred (see p. 132). A more fundamental alteration of the genome is probably indicated by the appearance of such new features as comarginal lamellae and radial striae and, in the absence of ancestral allometry, by the higher I_R/L of *C. (Cc.) obscurus*.

Within *C. (Cc.) obscurus* maximum height undergoes an overall phyletic increase in the passage from Aalenian (74 mm) to Bajocian (93.8 mm) to Bathonian (69 mm) to Tithonian (122 mm) to Valanginian (206 mm). The temporary reversal to the otherwise smooth trend in the Bathonian is undoubtedly a real phenomenon since a large number of specimens are available for measurement from the stage. There seems also to be a phyletic reduction in H/L from the Bathonian to Tithonian but the lack of data from intermediate stages precludes an assessment of whether or not evolution occurred gradually. Since H/L decreases during the ontogeny of ancestral populations the phyletic reduction in H/L could have been brought about by acceleration of shape development with respect to size.



Text fig. 131: *Camptonectes (Camptochlamys) clathratus* – height/length.

Camptonectes (Camptochlamys) clathratus (Roemer 1836)

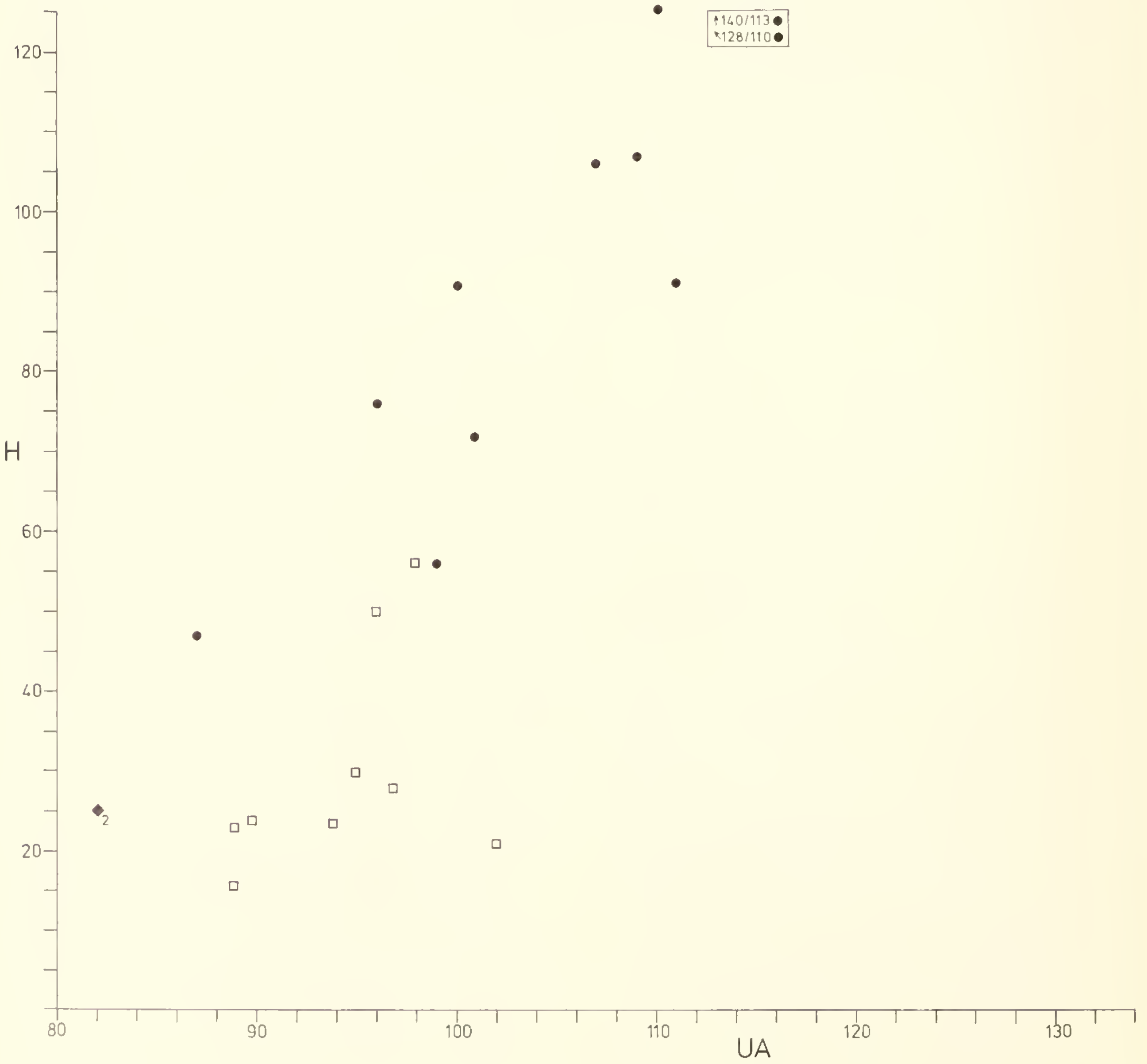
Pl. 4, Figs. 23, 26, 27, Pl. 5, Figs. 1–3, 6; text figs. 131–136

Synonymy

1836	*Pecten clathratus* sp. nov; Roemer, p. 212, pl. 13, fig. 9.
1839	*Pecten intertextus* sp. nov; Roemer, p. 27, pl. 18, fig. 23.
1842	*Pecten collineus* sp. nov; Buvignier in Sauvage and Buvignier, p. 533, pl. 4, fig. 7.
v*? 1850	*Pecten Rosimon* sp. nov; d'Orbigny, v. 1, p. 327 (Boule, 1913, v. 8, p. 92, pl. 2, figs. 26, 27).
v* 1852	*Pecten Michaelensis* sp. nov; Buvignier, p. 24, pl. 32, fig. 4.
v* 1853	*Pecten retiferus* sp. nov; Morris and Lycett, p. 9, pl. 1, figs. 15, 15a.
1853	*Pecten personatus* Goldfuss; Morris and Lycett, p. 11, pl. 1, fig. 17 (non fig. 17a, non Goldfuss sp.).
1853	*Pecten clathratus* Roemer; Morris and Lycett, p. 13, pl. 1, figs. 19, ?19a.
1860	*Pecten clathatrus* Roemer; Coquand, p. 79.
1862	*Pecten pertextus* sp. nov; Étallon in Thurmann and Étallon, p. 257, pl. 36, fig. 7.
1862	*Pecten Frotei* sp. nov; Étallon in Thurmann and Étallon, p. 258, pl. 36, fig. 9.
1863	*Pecten Michaelensis* Buvignier; Lycett, p. 34, pl. 33, fig. 3.
1863	*Pecten intertextus* Roemer; Dollfus, p. 81, pl. 15, figs. 1–3.
1867	*Pecten retiferus* Morris and Lycett; Laube, p. 10.
1875	*Pecten intertextus* Roemer; de Loriol and Pellat, p. 200, p. 23, fig. 2.
1893	*Pecten intertextus* Roemer; de Loriol and Lambert, p. 138, pl. 11, figs. 8, 8a.
1894	*Pecten intertextus* Roemer; de Loriol, p. 40.
1904	*Pecten intertextus* Roemer; de Loriol, p. 216.
1905	*Pecten (Chlamys) retiferus* Morris and Lycett; Kilian and Guébhard, p. 758.
1905	*Pecten intertextus* Roemer; Peron, p. 219.
non 1906	*Chlamys rosimon* (d'Orbigny); Cossmann, p. 4, pl. 1, figs. 7–9.

1906 *Chlamys retifera* (Morris and Lycett; Cossmann, p. 5, pl. 1, figs. 10, 11.
1907a *Chlamys retifera* (Morris and Lycett); Cossmann, p. 240, pl. 8, figs. 14, 15.
1923 *Chlamys Lafayi* sp. nov; Lissajous, p. 159, pl. 30, figs. 1, 2.
v non 1926 *Chlamys Rosimon* (d'Orbigny); Staesche, p. 38, pl. 2, fig. 1.
v 1930a *Chlamys (Camptochlamys) intertextus* (Roemer); Arkell, p. 103, pl. 8, figs. 1, 2.
? 1931 *Pecten (Chlamys) pertextus* var. *densiradiatus* var. nov; Sokolov and Bodylevsky, p. 54, pl. 3, figs. 6a, 6b.
(?) 1936 *?Camptochlamys Rosimon* (d'Orbigny); Dechaseaux, p. 38.
1936 *Camptochlamys retiferus* (Morris and Lycett); Dechaseaux, p. 39.
1936 *Camptochlamys Lafayi* (Lissajous); Dechaseaux, p. 39.
1936 *Camptochlamys intertextus* Roemer; Dechaseaux, p. 39.
1948 *Camptonectes (Camptochlamys) intertextus* (Roemer); Cox and Arkell, p. 14.
(?) 1948 *Camptonectes (Camptochlamys) rosimon* (d'Orbigny); Cox and Arkell, p. 14.
? 1961 *Camptonectes rigidus* (J. Sowerby); Rossi Ronchetti and Fantini Sestini, p. 122, pl. 13, figs. 1, 2 (non J. Sowerby sp.).
1961 *Camptochlamys retiferus* (Morris and Lycett); Barbulescu, p. 701.
1961 *Camptochlamys intertextus* (Roemer), Barbulescu, p. 701.
1964 *Camptonectes retiferus* (Morris and Lycett); J.-C. Fischer, p. 19.
? 1977 *Camptonectes (Camptochlamys)* cf. *intertextus* (Roemer); Kelly, p. 88, pl. 1, figs. 18a–c, 19, 20.

The holotype (M) of *Pecten clathratus* Roemer 1836, p. 212, pl. 13, fig. 9 is probably in the Roemer-Pelizaeus-Museum, Hildesheim, W. Germany. It was derived from the Oxfordian of N. Germany.



Text fig. 132: *Camptonectes (Camptochlamys) clathratus* – height/umbonal angle.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

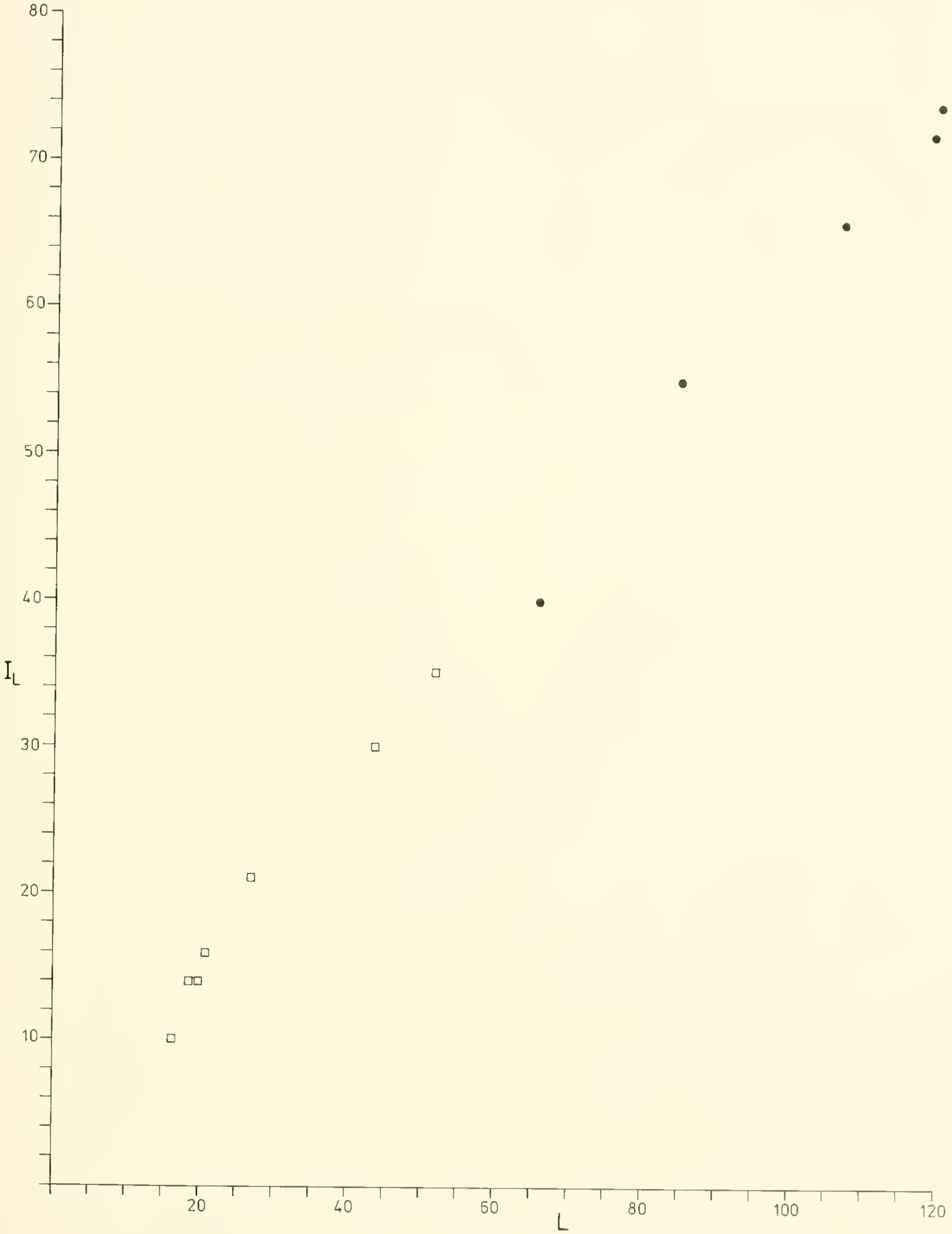
'P. testa lineis capillaribus acutis radiantibus rectis concentricisque regulariter clathrata, interstitiis planis quadratis.

Die ziemlich dünne Schale scheint fast kreisrund gewesen zu sein und trägt oben zahlreiche, haarförmige, schief in die Höhe gerichtete, gleich weit von einander stehende Linien, von den gerade ausstrahlende mit concentrischen ein sehr zierliches, feines Gitterwerk bilden. Die viereckigen, meist mehr breiten als hohen Flächen zwischen den Linien sind ganz flach.

Das abgebildete Bruchstück fand sich im oberen Coral rag des Spitzhuts mit *Terebr. tetragona* und *Turbo princeps* zusammen.'

2. AMENDED DIAGNOSIS

Distinguished from *C. (Cc.) obscurus* by the fact that the radial striae reach the ventral margins at all stages in ontogeny.



Text fig. 133: *Camptonectes (Camptochlamys) clathratus* – intersinal distance on left valve/length.

3. AMENDED DESCRIPTION

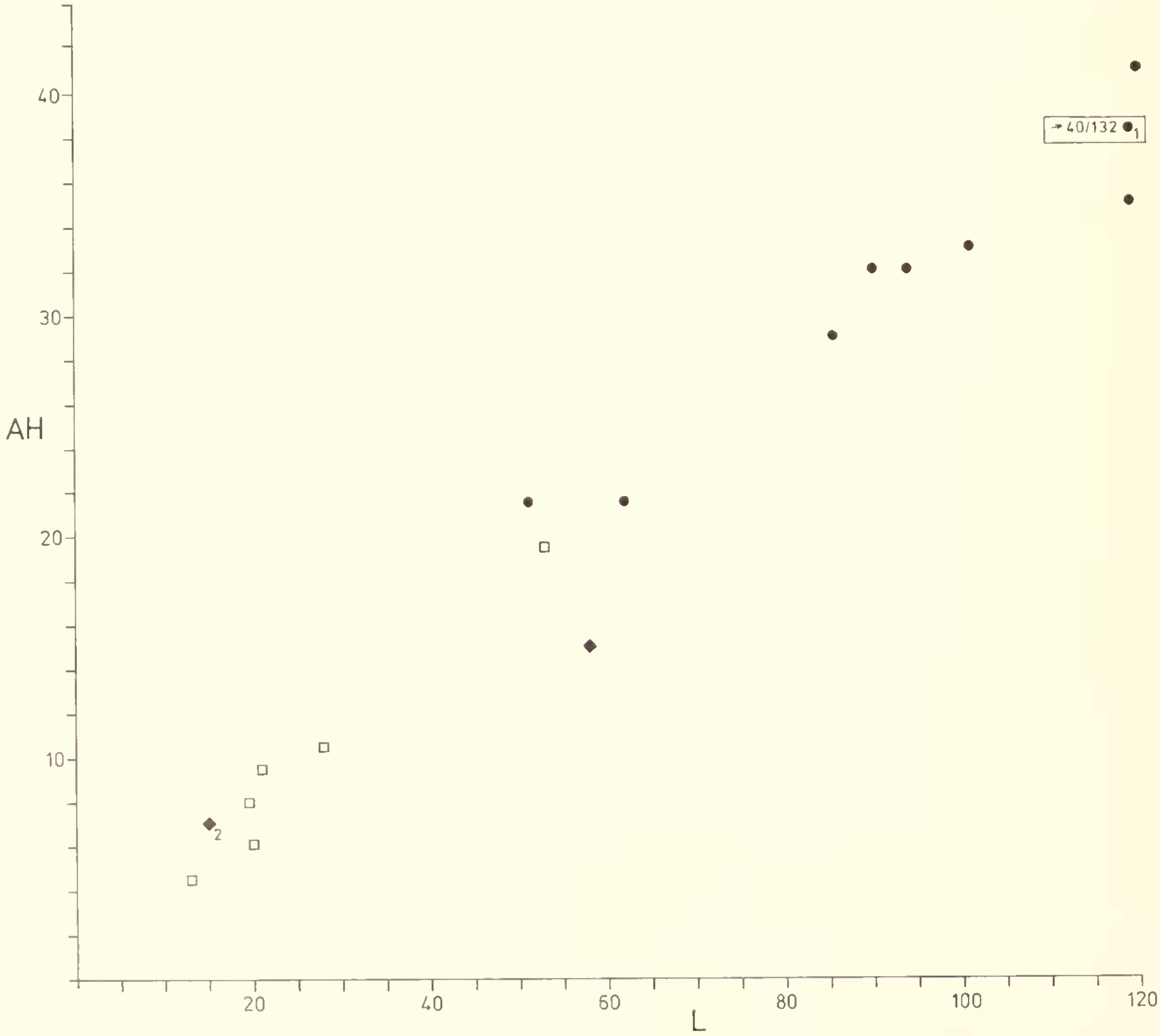
Essentially similar to *C. (Cc.) obscurus* apart from the diagnostic feature (see Section 2), possibly somewhat higher mean H/UA (text fig. 132), apparent allometric decrease in AH/L and I_L/L (text figs. 134, 133), lower comarginal lamellae and usual lack of divaricate striae (see p. 133). There are between 33 and 45 radial striae on the left valve and between 45 and 68 on the right valve (Pl. 4, Figs. 23, 26, 27, Pl. 5. Figs. 1–3, 6).

Other metric proportions are plotted in text figs. 131, 135.

4. DISCUSSION

As for *C. (Camptochlamys) obscurus* the disjunct stratigraphic range of the species described in Section 3 combined with a failure to appreciate the range of ornamental variation has led to the evolution of two taxonomic schemes for M. and U. Jurassic representatives. ARKELL (1930a) considered that Oxfordian specimens (referred to *'Chlamys' (Cc.) intertextus* (ROEMER)) differed from Bathonian specimens (referred to *'Ch.' (Cc.) retiferus* (MORRIS and LYCETT)) by the possession of 45–50 compared with 35–40 radial striae. Since ARKELL failed to recognise the disparity in numbers of striae between right and left valves this gives an incomplete picture of variation. However, if one assumes that counts were taken only from left valves, as seems likely, then the existence of Oxfordian specimens with 40 striae (e. g. YM 557) and Bathonian specimens with 45 striae (e. g. BM 65901) clearly contradicts ARKELL's hypothesis. Metric proportions offer no other grounds for a distinction, the larger Oxfordian forms plotting within the range of extrapolated Bathonian ontogenies (text figs. 131–135). Moreover the figured original of *'Pecten' intertextus* ROEMER, although only a broken specimen, is indistinguishable from the lectotype of *'P.' retiferus* MORRIS and LYCETT (IGS 9169; Pl. 4, Fig. 26).

On the basis of the preceding discussion the Oxfordian species *'P.' pertextus* ÉTALLON and *'P.' Michaelensis* BUVIGNIER (both described as having finer ornament than *'P.' intertextus*) cannot be separated from the species described in Section 3. In addition the figured original of *'P.' Michaelensis* (ENSM L340; Pl. 5, Fig. 3) has metric proportions (1) which plot within the range of projected ontogenies of the species described in Section 3. *'Ch.' Lafayi* LISSAJOUS was separated from *'P.' Michaelensis* only by a difference in ornament at large sizes. Since the figured original of the latter species turns



Text fig. 134: *Camptonectes (Camptochlamys) clathratus* – anterior hinge length/length.

out to be a large abraded specimen this is an insufficient basis for a specific distinction.

The present author has been unable to trace the original reference to *'P.' collineus* BUVIGNIER but ARKELL (1930a) places the species in synonymy with *'Ch.' (Cc.) intertextus*. *'P.' Frotei* ÉTALLON was compared with *'P.' collineus* in the original description and metric proportions of the original figure (2) plot within the range of the species described in Section 3.

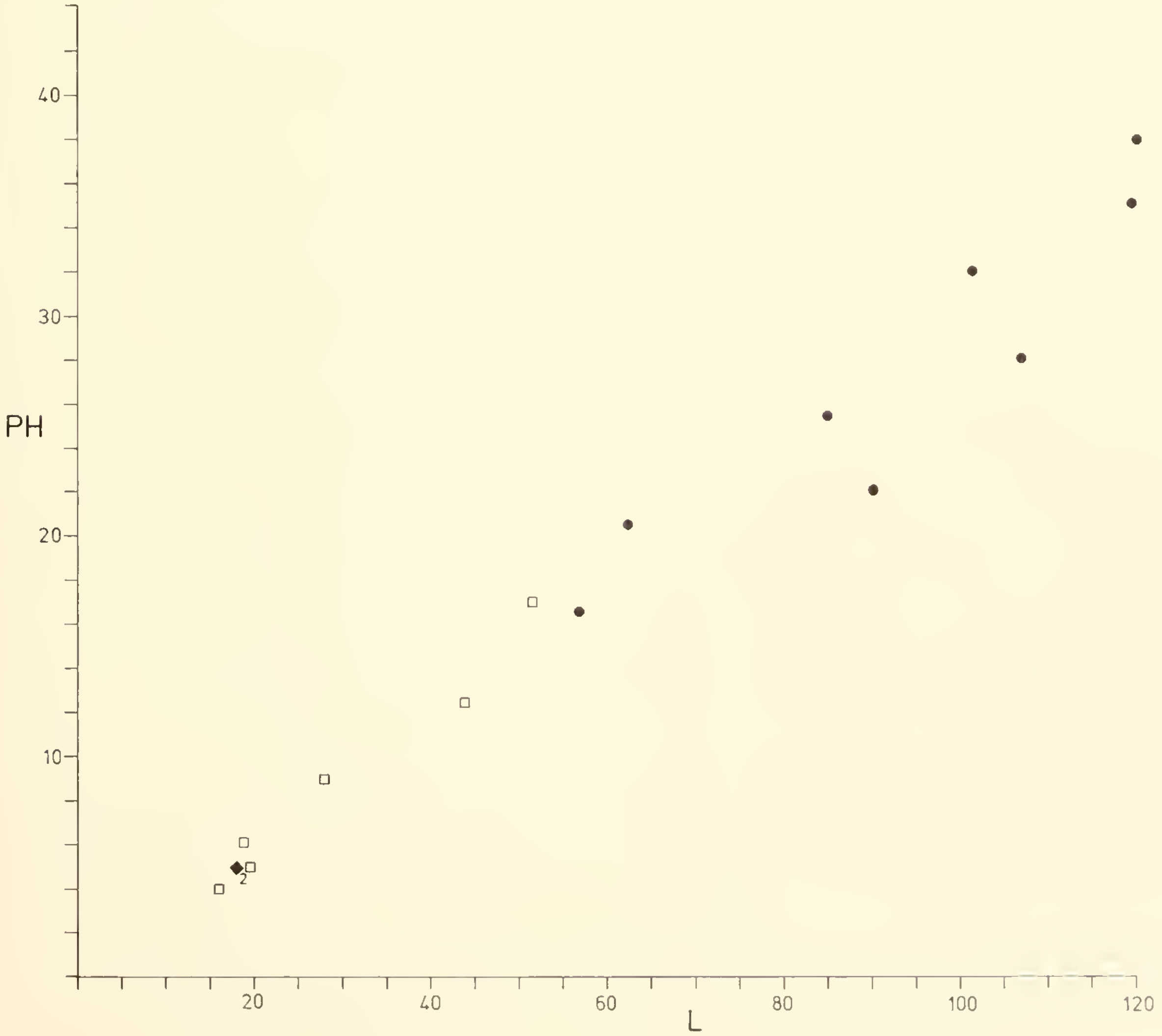
The holotype (M) of *'P.' Rosimon* D'ORBIGNY (MNO 2905) is a poor specimen whose large number of radial striae suggests that it may be referable to *Radulopecten vagans* (the interpretation followed by COSSMANN [1906]) rather than the species described in Section 3 (the interpretation apparently followed by DECHASEAUX [1936] and COX and ARKELL [1948]). The specimen (GPIT 1592/5; Pl. 8, Fig. 16) referred to *'Ch.' rosimon* by STAESCHE (1926) is much more strongly ornamented than D'ORBIGNY's holotype and belongs in *Ch. (Ch.) textoria*.

Of the species considered to be synonymous above, *'P.' intertextus* ROEMER was the first designated. However, an earlier species *'P.' clathratus* ROEMER has the characteristic reticulate ornament of the species described in Section 3 and although only described from a fragment must be given historical precedence. One of MORRIS and LYCETT's (1853) figures of *'P.' clathratus* (pl. 1, fig. 19) is indistinguishable from ROEMER's species but the other (pl. 1, fig. 19a) is more reminiscent of *C. (C.) laminatus*. The same authors also figure an example of ROEMER's species (pl. 1, fig. 17) under the non-synonymous specific name *'P.' personatus* GOLDFUSS (see p. 24). The other figured example of *'P.' personatus* (pl. 1, fig. 17a) may be referable to *C. (C.) laminatus*. A specimen referred to the non-synonymous species *C. rigidus* (J. SOWERBY) by ROSSI RONCHETTI and FANTINI SESTINI (1961) is discussed on p. 127.

KELLY's (1977) record of *C. (Cc.)* cf. *intertextus* from the M. Volgian can only tentatively be placed in synonymy because the small size of his specimens allows the possibility of confusion with juveniles of *C. (Cc.) obscurus*, a common species at this horizon. Similar reasoning applies to the tentative inclusion of *'P.' (Ch.) pertextus* var. *densiradiatus* SOKOLOV and BODYLEVSKY (1931).

5. STRATIGRAPHIC RANGE

Two specimens (BM LL1593, LL23688) from the Bajocian of S. England are probably referable to *C. (Cc.) clathratus* as



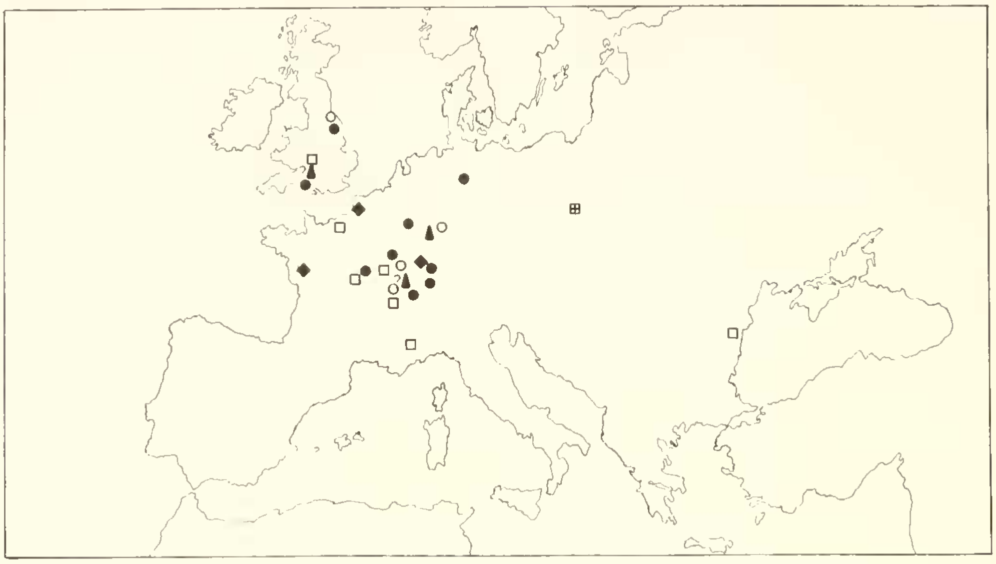
Text fig. 135: *Camptonectes (Camptochlamys) clathratus* – posterior hinge length/length.

are a number of specimens from the U. Bajocian in DM. Dechaseaux (1936) records an indeterminate number of specimens from the Bajocian of the E. Paris Basin. In the appropriate facies (see Section 8) the species is quite common in the Bathonian but it becomes rare again in the Callovian. Two specimens are known from the U. Cornbrash of Yorkshire (YM 592, BM 47434), a few specimens reside in DM,and Dechaseaux (1936) records an indeterminate number of specimens from the Callovian of the E. Paris Basin. The species is locally quite common in the Oxfordian but becomes rare in the Kimmeridgian, unequivocal records being limited to NW France (BM 25346, 65895; Dollfus, 1863), W. France (one specimen, author's collection) and the Jura (Thurmann and Étallon, 1862).

Kelly (1977) records nine specimens, which may be referable to *C. (Cc.) clathratus* (see Section 4) from the M. Volgian (M. Tithonian) of Lincolnshire.

6. GEOGRAPHIC RANGE

C. (Cc.) clathratus occurs widely in northern and central Europe (text fig. 136), its local distribution and abundance being largely controlled by the development of the appropriate sedimentary facies (see Section 8). Records outside Europe are limited to two dubious specimens (see Section 4), one from Afghanistan (Rossi Ronchetti and Fantini Sestini, 1961) and the other from Spitzbergen (Sokolov and Bodylevsky, 1931).



Text fig. 136: *Camptonectes (Camptochlamys) clathratus* – European distribution.

7. DESCRIPTION OF ECOLOGY

In the Bathonian of England *C. (Cc.) clathratus* is found quite commonly in the Minchinhampton Beds (L. Bathonian) where it reaches a maximum height of 57.5 mm (BM LL1593). The sediments are grain supported shelly oolites containing a diverse gastropod and bivalve fauna, including *C. (Cc.) obscurus* (Morris and Lycett, 1851–55). The species is also quite common in the roughly contemporaneous Calcaire à Polypiers of Normandy and occurs in a coral bed in Indre with *Spondylopecten (S.) palinurus* and the 'coarse' phenotype of *Chlamys (Ch.) textoria* (Cossmann, 1907a; J.-C. Fischer, 1964).

In the Oxfordian of Yorkshire large specimens of *C. (Cc.) clathratus* occur in the Malton Oolite (Plicatilis zone), reaching a maximum height of 140 mm (YM 492D). The sediments are oolites, usually poorly fossiliferous, but locally containing coral debris and such bivalves as the 'coarse' phenotype of *Ch. (Ch.) textoria*, *Lima*, *Exogyra*, *Opis*, *Gervillia* and *Trichites*, together with the gastropod *Pseudomelania* (J. Wright, 1972). *C. (Cc.) clathratus* is rare in contemporaneous oolites on the Dorset coast (Osmington Oolite) in which coral debris is absent. The species is reported to be common in reef and reef-derived sediments in the Yonne (Peron, 1905) and records from the Oxfordian of the Meuse (Buvignier, 1852), Jura (de Loriol, 1894, 1904) and L. Saxony (Roemer, 1836) are from a similar facies,as may be records from the Kimmeridgian of the Jura (Thurmann and Étallon, 1862). The author has collected a specimen from Kimmeridgian marls adjacent to patch reefs at La Rochelle (Charente Maritime).

Other records of *C. (Cc.) clathratus* consist of small or indeterminate numbers of specimens.

8. INTERPRETATION OF ECOLOGY

The usual occurrence of *C. (Cc.) clathratus* in oolitic and reefal deposits indicates a preference for environments of high energy. The rarity of the species in the Callovian and Kimmeridgian of northern and central Europe (see Section 5) and throughout the M. and U. Jurassic in southern Europe (see Section 6) can thus be viewed as a consequence of the widespread development of low energy, clay-grade facies.

In the U. Jurassic of continental Europe there is a clear correlation between the distribution of coral reef facies and that of *C. (Cc.) clathratus*. Although the species occurs in oolites in the Oxfordian of Yorkshire, the occasional presence of corals and a reef-derived fauna may indicate that a substantial reef existed nearby (J. Wright, 1972) and thus an association with this facies for at least part of the life history cannot be ruled out. The rarity of *C. (Cc.) clathratus* in contemporaneous non-coralliferous oolites in Dorset is evidence that such sediments alone could not induce colonisation of an area by *C. (Cc.) clathratus*. There are however few grounds for invoking the presence of unexposed reefs to explain the occurrence of *C. (Cc.) clathratus* in Bathonian oolites at Minchinhampton, although the recent discovery (Ager et al., 1973) of *Isastrea* and *Thamnasteria* should be noted. A clearer association with corals, if not with coral reefs, is indicated by occurrences in Normandy and Indre, and the presence in the latter area of pectinids which were at least able to colonise reefs is worth pointing out.

It can be summarised from the foregoing that there is a strong correlation between the occurrence of *C. (Cc.) clathratus* und coralliferous deposits and that numbers may be highest in the vicinity of coral accumulations of reefal dimensions. It could be that level bottom environments adjacent to coral stands were inhabited when byssal fixation to corals became impossible in the later stages of ontogeny (see Section 9).

Since *C. (Cc.) clathratus* occurs with a high diversity fauna in, at most, moderate numbers, it was probably an equilibrium species (Levinton, 1970).

Other species of *Camptonectes* including the probable ancestor *C. (Cc.) obscurus* (q. v.) show little sign of having competed with *C. (Cc.) clathratus*.

9. FUNCTIONAL MORPHOLOGY

Since *C. (Cc.) clathratus* is in most morphological respects identical to *C. (Cc.) obscurus*, a juvenile byssate followed by an adult reclining mode of life can be similarly inferred. Corals probably constituted the favourite site for byssal attachment and oolites seem to have been preferred for the reclining phase (see Section 8).

10. ORIGINS AND EVOLUTION

The most likely ancestor for *C. (Cc.) clathratus* is *C. (Cc.) obscurus*. Since the radially striate ornament characteristic of adult representatives of the former species is present in juveniles of the latter trans-specific evolution could have been largely brought about by the heterochronic retardation of shape development with respect to size. As *C. (Cc.) clathratus* first occurs within the geographic range of *C. (Cc.) obscurus* the possibility of sympatric speciation cannot be entirely ruled out. It may be that speciation followed after a few individuals of *C. (Cc.) obscurus* switched to corals for juvenile byssal attachment, whence disruptive selection and establishment of a stable polymorphism ensued (cf. Tauber and Tauber, 1977a, b).

Within *C. (Cc.) clathratus* there is a marked increase in maximum height from the Bathonian (57.5 mm) to the Oxfordian (140 mm) although the paucity of intermediate records precludes an assessment of wether or not this represents a gradual trend. Phyletic increase in size combined with a neotenous origin are strong indicators of the prevalence of 'K' selection (Gould, 1977).

Genus *EOPECTEN* Douvillé 1897

(Synonyms etc. *Velata* Quenstedt 1856 [non Griffith and Pidgeon 1934, obj.]
Velopecten Philippi 1899 [pro *Velata* Quenstedt 1856, non *Velates* Montfort 1810]
Velatopecten Rollier 1906 [nom. van.])

Type species. OD; Douvillé 1897, p. 203; *Hinnites tuberculatus* Goldfuss errore pro *Spondylus tuberculosus* Goldfuss 1836, p. 93, pl. 105, fig. 2; Aalenian/Bajocian, Swabia.

AMENDED DIAGNOSIS

Medium sized to large, acline, more or less irregular in outline at all stages of growth, some specimens irregularly puckered or with allomorphic ornament; inequivalve, with LV convex and RV flat or concave; left anterior wing large, indistinctly demarcated, right anterior auricle elongate, deep subauricular notch with ctenolium below it; posterior wing rather small; RV with narrow, obtusely triangular cardinal area with deep, narrowly triangular pit below beak corresponding to resilium (same in LV); interior of RV in some specimens with blunt oblique internal ridge originating near resilifer; ornament of striae and costae of varying strengths. L. Jur. (Hettang.)-L. Cret. (Alb.), cosmop.

DISCUSSION

In his diagnosis Hertlein (1969: N373) implied that *Eopecten* was cemented early in ontogeny. The present author can find no positive evidence for this. The hinge characteristics of the left valve, unknown to Hertlein, are now clear.

The immense variability within *Eopecten*, at least some of which is demonstrably ecophenotypic (see p. 154), has resulted in the designation of a plethora of specific names by typological authors. Rollier (1915) alone cites 51 species from the Mesozoic of central W. Europe. Such numbers seem highly improbable in the light of analyses of Recent communities and with the evidently slow rate of species turnover in the Pectinidae. However, it remains difficult to evaluate the extent of ecophenotypic 'noise' in order to delineate true species. An analysis along the lines adopted for *Radulopecten vagans* (see Johnson, 1981) might prove instructive although sampling problems would undoubtedly be great. In the lack of such an analysis the author has been forced to adopt a more subjective approach.

Ornamental variation in left valves appears to be distributed around three modal patterns, distinguished as follows:

1. Ornament clearly differentiated into costae and striae in all but very large specimens.

2. Intercalary costae rapidly gaining the same size as original costae which are themselves of approximately equal size.
3. Intercalary costae rapidly gaining the same size as original costae but two of latter greatly enlarged and bearing tubercles.

Since, at any one locality, there is a marked tendency for only one of the modal patterns (and variants thereof) to be present it may be that the modes themselves represent ecophenotypic variants and that therefore all Jurassic *Eopecten* should be placed in a single species. However, in the lack of a statistical analysis of ontogeny (see above) and of an adaptive reason for such ecophenotypic variation it is preferred herein to treat the three modes as being indicative of three separate species (respectively *E. velatus*, *E. spondyloides* and *E. abjectus*) and to assume that the mutual exclusion at any one locality is due to inter-specific competition.

There is some suggestion, based on the number of costae (see p. 152), that forms grouped around mode 1 may themselves be divisible into two groups. However, until separate contemporaneous lineages can be demonstrated the author prefers to attribute such differences as do exist to phyletic evolution within a single species.

Due to the difficulties in defining *Eopecten* species at the outset comprehensive descriptions or figures have to be available (in the absence or non-availability of type material) before a taxonomic species can be assigned to one of the above groups. Consequently a number of rather poorly characterised taxonomic species of *Eopecten* have had to be left out of the synonymy lists pending examination of type material. These include: in Goldfuss (1836), *'Hinnites' tenuistriatus* Münster; in Tietze (1872), *'H.' sublaevis;* in Gemmellaro and Di Blasi (1874), *'H.' Waageni;* in Gemmellaro (1878), *'H.' ctenopsides, 'H.' aracnoides;* in Blaschke (1911), *'P.' kotoucensis;* in Rollier (1915), *'H.' ('Prospondylus') Greppini, 'H.' ('Pr.') ferrugineus, 'H.' ('Pr.') Dollfusi, 'H.' ('Pr.') Argoviensis, 'H.' ('Terquemia') Censoriensis;* in Paris and Richardson (1916), *Eopecten doultingensis;* in De Gregorio (1922); *'Pecten' flexocostulatus.*

Eopecten velatus (Goldfuss 1833)

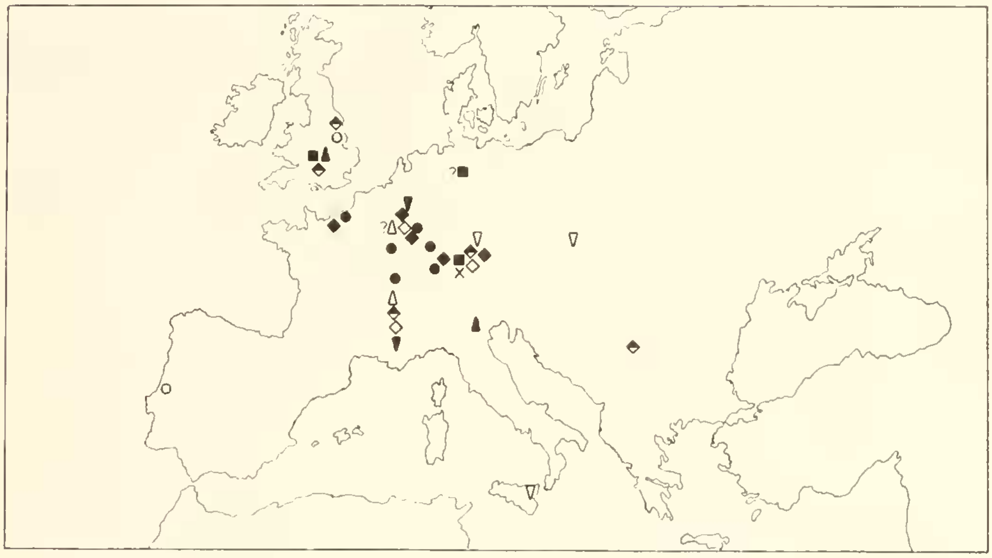
Pl. 5, Figs. 4, 5, 7, 8; text figs. 137–141

Synonymy

1833 *Pecten velatus* sp. nov; Goldfuss, p. 45, pl. 90, fig. 2.
1833 *Pecten tumidus* sp. nov; Hartmann in v. Zieten, p. 68, pl. 52, fig. 1.
1836 *Lima inaequistriata* sp. nov; Goldfuss, p. 81, pl. 114, fig. 10.
1836 *Spondylus velatus* sp. nov; Goldfuss, p. 94, pl. 105, fig. 4.
v* 1850 *Hinnites inaequistriatus* sp. nov; d'Orbigny, v. 2, p. 22.
non 1853 *Hinnites velatus* (Goldfuss); Morris and Lycett, p. 14, pl. 2, figs. 2, 2a.
v 1858 *Pecten velatus* Goldfuss; Quenstedt, p. 148, pl. 18, fig. 26, p. 184, pl. 23, fig. 3.
1858 *Pecten velatus albus* subsp. nov; Quenstedt, p. 628, pl. 78, fig. 3.
non 1862 *Pecten velatus* (Goldfuss); Thurmann and Étallon, p. 266, pl. 37, fig. 12.
1862 *Hinnites inaequistriatus* d'Orbigny; Thurmann and Étallon, p. 267, pl. 37, fig. 13.
1863 *Hinnites Hautcoeuri* sp. nov; Dollfus, p. 86, pl. 17, figs. 1, 2.
non 1864 *Hinnites velatus* (Goldfuss); Dumortier, p. 70, pl. 4, figs. 1–3.
1869 *Hinnites Davaei* sp. nov; Dumortier, p. 141, pl. 21, figs. 9, 10.
1872 *Hinnites inaequistriatus* d'Orbigny; de Loriol et al., p. 391, pl. 23, fig. 2.
1872 *Hinnites velatus* (Goldfuss); Tietze, p. 108, pl. 3, fig. 2.
1874 *Hinnites velatus* (Goldfuss); Dumortier, p. 308, pl. 62, figs. 3, 4 (non p. 195, pl. 43, fig. 6).
1874 *Hinnites thurmanni* sp. nov; Brauns, p. 343.
1874 *Pecten hinnitiformis* sp. nov; Gemmellaro and Di Blasi, p. 117, pl. 2, figs. 16–19.
1875 *Pecten hinnitiformis* Gemmellaro and Di Blasi; Gemmellaro, p. 49.
1876 *Hinnites tumidus* (Hartmann); Tate and Blake, p. 365.
1878 *Hinnites astartinus* Greppin; de Loriol, p. 163, pl. 23, fig. 3.
1881a *Hinnites inaequistriatus* d'Orbigny; Boehm, p. 181, pl. 40, fig. 1.
1881a *Hinnites gigas* sp. nov; Boehm, p. 182, pl. 40, figs. 11, 12.
1881a *Hinnites subtilis* sp. nov; Boehm, p. 182, pl. 40, fig. 4.
1883 *Hinnites* cf. *astartinus* Greppin; Boehm, p. 619, pl. 68, figs. 7, 8.
non 1886d *Hinnites velatus* var. *irgetus* var. nov; De Gregorio, p. 20, pl. 13, figs. 1–6.
1886 *Pleuronectites Aubryi* sp. nov; Douvillé, p. 228, pl. 12, fig. 3.
1903 *Velopecten* cf. *astartinus* (Greppin); Remes, p. 207, pl. 19, fig. 13.
1903 *Velopecten* cf. *inaequistriatus* (d'Orbigny); Remes, p. 207, pl. 20, fig. 1.
1904 *Hinnites Bonjouri* sp. nov; de Loriol, p. 231, pl. 25, figs. 1, 2.
1905 *Hinnites inaequistriatus* (d'Orbigny); Peron, p. 238.
1915 *Hinnites (Prospondylus) Dumortieri* sp. nov; Rollier, p. 452.
1915 *Hinnites (Prospondylus) Quenstedti* sp. nov; Rollier, p. 453.
1915 *Hinnites (Prospondylus) Toarciensis* sp. nov; Rollier, p. 453.
1915 *Hinnites (Prospondylus) ammoniticus* sp. nov; Rollier, p. 461, pl. 30.
1915 *Hinnites (Prospondylus) Orbignyi* sp. nov; Rollier, p. 464.
1916 *Eopecten Dumortieri* sp. nov; Cossmann, pp. 48, 49, text figs. 1, 2.
non 1926 *Velopecten velatus* (Goldfuss); Arkell, p. 549, pl. 34, fig. 6.
v 1926 *Velopecten tumidus* (Hartmann); Staesche, p. 117, pl. 4, fig. 7, pl. 5, fig. 4.
v 1926 *Velopecten velatus* (Goldfuss); Staesche, p. 122, pl. 6, fig. 11.
1928 *Velata velata* (Goldfuss); Cox, p. 244.
1933 *Velata inaequistriata* (d'Orbigny); Dietrich, p. 67, pl. 8, fig. 129.
1935 *Entolium hauptsmoorii* sp. nov; Kühn, p. 469, pl. 18, figs. 2a–c.
1935b *Velata velata* (Goldfuss); Cox, p. 4, pl. 1, figs. 2, 3.
v 1936 *Velata Bonjouri* (de Loriol); Dechaseaux, p. 70, pl. 8, fig. 14.
1936 *Velata Hettangiensis* sp. nov; Dechaseaux, p. 71, pl. 9, fig. 1.

1936 *Velata tumidus* (HARTMANN); KÜHN, p. 250, pl. 11, fig. 2.
1939 *Velata aubryi?* (DOUVILLÉ); STEFANINI, p. 186, pl. 20, figs. 10, 11, pl. 21, fig. 1.
1952 *Eopecten aubryi* (DOUVILLÉ); COX, p. 52, pl. 6, figs. 3, 4.
1965 *Eopecten aubryi* (DOUVILLÉ); COX, p. 52, pl. 6, figs. 3, 4.
1965 *Eopecten thurmanni* (BRAUNS); COX, p. 53, pl. 6, fig. 8.
1965 *Eopecten* aff. *albus* (QUENSTEDT); COX, p. 54, pl. 6, fig. 7.
non 1973 *Chlamys (Velata)* cfr. *velata* (GOLDFUSS); LENTINI, p. 29, pl. 15, fig. 8.

Neotype of *Pecten velatus* GOLDFUSS, p. 45, pl. 90, fig. 2 herein designated; GPIT 1592/2; Pl. 5, Fig. 7 herein; L. Pliensbachian, Eslingen, S. Germany.



Text fig. 137: *Eopecten velatus* – European distribution.

Text fig. 138: *Eopecten velatus* – World distribution (Pliensbachian reconstruction).

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

'*Pecten* testa obliqua ovato-orbiculari convexa, costis linearibus distantibus (14) minoribus totidem intermediis lineisque pluribus interstitialibus, lineis concentricis subtilissimus confertis, auriculis inaequalibus decussatim lineatis.

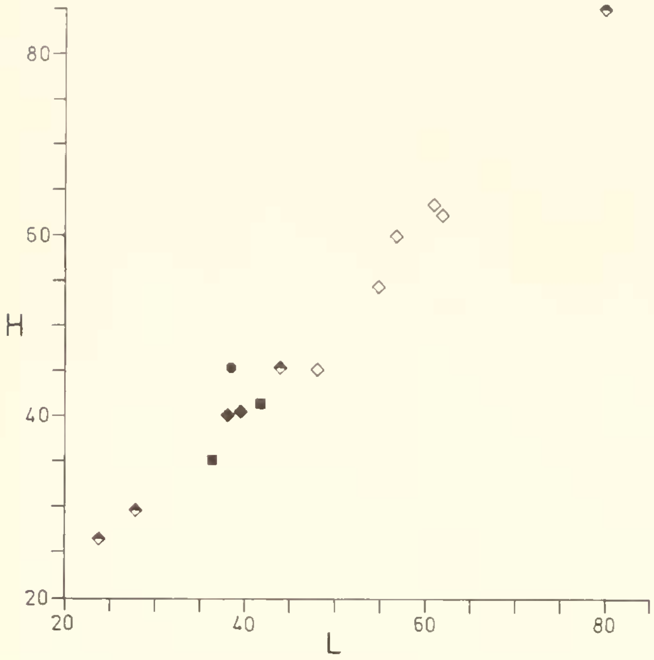
E montibus Herciniae et Palatinatus superioris. M. B. M. M.

Schief eiförmig-kreisrund, flach-convex, mit 14 linienförmigen Rippen, mit welchen eben so viel etwas niedrigere, abgekürzte, abwechseln. Die Zwischenräume sind mit 2–3 feinen Linien ausgefüllt, und die ganze Fläche mit sehr zarten, gedrängten, concentrisch Linien gegittert. Die ungleichen Ohren haben ähnliche Rippen und Linien, und verlaufen sanft ansteigend gegen die Höhe des Wirbels.

Findet sich bei Quedlinburg, Bayreuth und Amberg.'

2. AMENDED DIAGNOSIS

Distinguished from other species of *Eopecten* by the differentiation of the ornament on the left valve into costae and striae in all but very large specimens (e. g. BM 65900; Pl. 5, Fig. 8).



Text fig. 139: *Eopecten velatus* – height/length.

3. AMENDED DESCRIPTION

Disc shape extremely variable, often irregular (Pl. 5, Fig. 4), generally longer than high (text fig. 139), maximum height 110 mm (OUM J14501). Umbonal angle variable (text fig. 140) usually increasing during ontogeny. Disc flanks low. Approximately equilateral to markedly inequilateral; inequivalve, right valve usually flat, left valve low to high convexity.

Intersinal distance greater in left valve than right, very large byssal notch with well developed ctenolium.

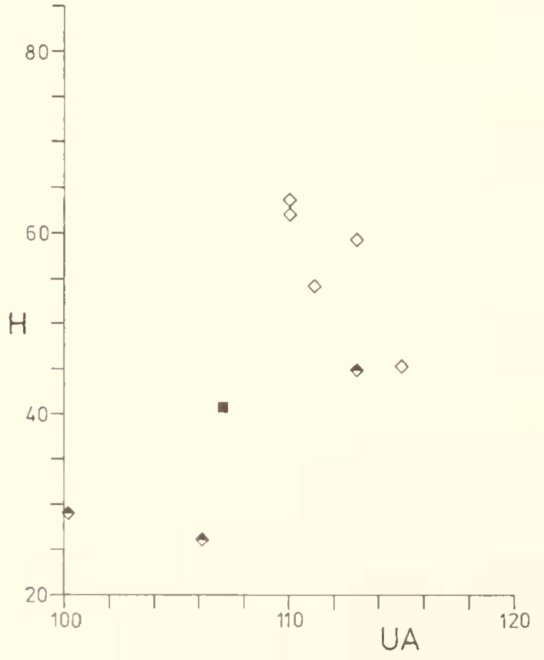
Auricles poorly demarcated from disc, variable in size, usually large with anterior (text fig. 141) larger than posterior. All auricles meeting hinge line at about 90°. Anterior auricle of left valve and both posterior auricles meeting disc at an acute angle. Anterior auricle of right valve meeting disc at an obtuse angle.

Right valve bearing a large number (< 150) of fine radial striae (Pl. 5, Fig. 5). Ornament of left valve very variable, usually comprising between 15 and 20 (range 5–28) original radial costae (see Section 4) between each pair of which are 4–6 (range 2–8) fine radial striae. Both costae and striae of variable height and often sinuous (Pl. 5, Figs. 4, 7, 8).

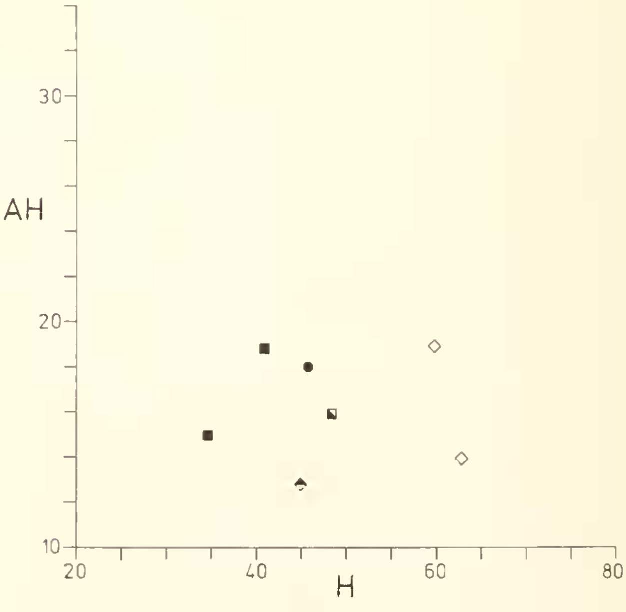
Shell thickness variable, left valve usually thicker than right.

4. DISCUSSION

Specimens possessing the diagnostic features of Section 2 which have been described from the L. Jurassic have a minimum of 14 (*'Pecten' velatus* GOLDFUSS) and a maximum of 24 (*'Hinnites' Davaei* DUMORTIER) costae on the left valve. Museum specimens of the same age usually possess between 15 and 20 costae. Specimens described from the U. Jurassic may have as few as 5 (*'H.' inaequistriatus* D'ORBIGNY; DE LORIOL et al.) or as many as 28 (*'P.' velatus albus* QUENSTEDT) costae. Moreover the large number of specimens which have been described with costal counts below the L. Jurassic range (e. g. *Eopecten thurmanni* (BRAUNS); COX with 8, *Velopecten* cf. *inaequistriatus* (D'ORBIGNY); REMES with 10, *'P.' hinnitiformis* GEMMELLARO and DI BLASI with 10–12, *'H.'* cf. *astartinus* DE LORIOL; BOEHM with 12 and *E.* aff. *albus* (QUENSTEDT); COX with 13) indicates that the mean number of costae may be less in U. compared with L. Jurassic



Text fig. 140: *Eopecten velatus* – height/umbonal angle.



Text fig. 141: *Eopecten velatus* – anterior hinge length/height.

samples. Specimens with costal counts within the L. Jurassic range do however exist (e. g. *'H.' astartinus* Greppin; de Loriol with 16, *'H.'* cf. *astartinus* Greppin; Boehm with 17 and *'V.' velatus* (Goldfuss); Staesche with 20) and in the absence of any evidence for a bimodal distribution suggest that the increase in range and possible reduction in mean number of costae is due to phyletic evolution within a single lineage. All forms possessing the diagnostic features of Section 2 are therefore included within the same species (see p. 150). Earlier authors labelled many individual variants of this species with a name thus a large number of synonymous taxonomic species have been generated. It seems futile to set down the peculiarities of each of these. Rather, those which are adequately characterised such that, in the author's opinion, they undoubtedly fall within the range of Section 3, are placed in synonymy and discussion is mainly limited to taxonomic problems. A large number of inadequately described or poorly illustrated secondary references to synonymous species are excluded from the synonymy and are not taken into consideration in subsequent sections. They may be traced in Quenstedt (1843, 1852), Oppel (1853, 1858), Coquand (1860), Trautschold (1861), Phillips (1871), Neumayr (1871), Terquem and Piette (1865), Brauns (1871, 1874), Tate and Blake (1876), Boehm (1881), Alth (1882), Roeder (1882), Simpson (1884), Kilian (1889), Botto-Micca (1893), Behrendsen (1893), Möricke (1894), Greppin (1898), Kilian and Guébhard (1905), Trauth (1909), Simionescu (1898, 1910), Paris and Richardson (1916), Faure-Marguerit (1920), Newton (1921), Blanchet (1923), Ernst (1923), Roman (1926), Lanquine (1929), Arkell (1930a), Yin (1931), Cox (1935a), Dechaseaux (1936), Parent (1940), Rakus (1964), Behmel and Geyer (1966), Urlichs (1966), Nitzopoulos (1974) and Yamani (1975). Lentini's (1973) record of *'Chlamys' ('Velata')* cfr. *velata* (Goldfuss) appears to be a misidentification of *Chlamys (Ch.) textoria.*

'Pecten' velatus Goldfuss and *'P.' tumidus* Hartmann, both described in 1833, appear to have equal claims to be the senior synonym of the species described in Section 3. However, Cox (1928) has pointed out that *'P.' tumidus* Hartmann is a junior primary homonym of *'P.' tumidus* Turton (1822) and is therefore not available. There is no trace of the type material to *'Pecten' velatus* in the Goldfuss Collections of the BSPHG and GPIB. A neotype (GPIT 1592/2; Pl. 5, Fig. 7) is therefore herein designated. Goldfuss (1836) also applied the name *velatus* to *Spondylus* but his figure is clearly of an *Eopecten* so this usage must be rejected as a junior secondary homonym. Cox (1965) raised Quenstedt's (1858) subspecies *'P.' velatus albus* to specific rank to act as a replacement name for comparable U. Jurassic forms. However, this manoeuvre is rendered superfluous by the present author's inclusion of both the 1833 and 1836 uses of *velatus* Goldfuss within the same hypodigm. Perhaps as a reaction to the evident taxonomic confusion a number of authors have applied the name *velatus* as a blanket term to all Jurassic *Eopecten.* Specimens so named in Morris and Lycett (1853), Thurmann and Étallon (1862), Dumortier (1964), De Gregorio (1886d) and Arkell (1926) together with some of the specimens (see Synonymy) so named in Dumortier (1874) are clearly representative of *E. spondyloides.*

The name *inaequistriatus* presents a similar case to that of *velatus.* Cox (1965) rejected *'H.' inaequistriatus* d'Orbigny (1850) as a junior secondary homonym of *'Lima' inaequistriata* Goldfuss (1836) since both species in fact belong to *Eopecten.* The specific name *thurmanni* Brauns was adopted for forms similar to d'Orbigny's species. However, this manoeuvre is rendered unnecessary by the present author's inclusion of d'Orbigny's and Goldfuss's species within the same hypodigm. It should be noted that the 1850 authorship of *inaequistriatus* should undoubtedly be credited to d'Orbigny rather than to Voltz as de Loriol et al. (1872), Boehm (1881), Remes (1903), Peron (1905) and Dietrich (1933) have assumed. Voltz's use of the name exists only in an unavailable manuscript form.

The original authorship of *'H.' astartinus* is that of Greppin rather than de Loriol, as Boehm (1883) and Remes (1903) have supposed, while the original authorship of *'P.' tumidus* should be attributed to Hartmann rather than v. Zieten as Tate and Blake (1876) have assumed.

Although they were not figured Rollier's (1915) species *'H.' ('Prospondylus') Quenstedti* and *'H.' ('Pr.') Toarciensis* can confidently be placed in synonymy because they were founded on specimens described in Quenstedt (1858) which are clearly referable to *E. velatus.* The same can be said for *'H.' ('Pr.') Orbignyi* and *'H.' ('Pr.') Dumortieri* which were based on specimens described in respectively Peron (1905) and Dumortier (1864).

5. STRATIGRAPHIC RANGE

The earliest certain records of *E. velatus* are from the Planorbis zone of the Rhone (Dumortier, 1864) and the Hettangian of Belgium (Dechaseaux, 1936). A few specimens are known from the Sinemurian of S. Germany (GPIT) and thereafter the species is relatively common at most horizons until the U. Toarcian. Aalenian records are limited to an indeterminate (probably small) number of specimens from the Rhone (Dumortier, 1874) and a single specimen from the E. Paris Basin (NM). Bajocian records are similarly limited to indeterminate numbers of specimens from Ethiopia (Douvillé, 1916) and Somalia (Stefanini, 1939), two specimens from N. Italy (BM L61819, L61820) and one from S. England (BM 50552). The species is unknown from the Bathonian but is recorded from the Callovian of NW India (Cox, 1952), E. Africa (Cox, 1965), Portugal (BM LL30871) and N. England (BM 47438). Unequivocal L. Oxfordian records are limited to a small number of specimens from E. Africa (Cox, 1965) but in the U. Oxfordian *E. velatus* occurs widely and is common in the Yonne (Peron, 1905). Thereafter the species occurs sporadically at most levels until the U. Tithonian (Boehm, 1883; Remes, 1903).

6. GEOGRAPHIC RANGE

In Europe (text fig. 137) *E. velatus* is a widespread species. The paucity of records from the M. Jurassic of Europe is temporally correlated with the appearance of the species in E. Africa and India (text fig. 138) and probably signifies a migration along the southern shores of Tethys, perhaps as a result of competitive exclusion by the common European species, *E. spondyloides* (see Section 8) and *E. abjectus.*

7. DESCRIPTION OF ECOLOGY

E. velatus is first recorded in any numbers from L. Pliensbachian clays, marls and limestones in S. Germany, where it reaches a maximum height of 63 mm (GPIT). In similar facies in the Margaritatus zone (U. Pliensbachian) of the same area the species attains a height of 64 mm (GPIT). However, in chamosite oolites of the Banbury Ironstone (Spinatum zone) a height of 110 mm (OUM J14501) is reached, although specimens are rare (assoc. fauna p. 16). In the widespread bituminous shale facies of the L. Toarcian *E. velatus* is similarly rare but in the U. Toarcian marls and limestones of S. Germany the species is relatively common, reaching a maximum height of 41 mm (GPIT). The associated fauna consists mainly of ammonites and belemnites. An isolated specimen from the Toarcian of France (BM 65900) reaches a height of 75 mm while in the M. Jurassic, when *E. velatus* is rare in Europe, a specimen from the Aalenian of France (NM) attains a height of 101 mm.

In the U. Oxfordian *E. velatus* is reported to occur commonly in reef limestones in the Yonne (Peron, 1905) where *E. spondyloides* seems to be rare (assoc. fauna p. 88). It also occurs in similar facies in the Jura, reaching a maximum height of 70 mm (de Loriol, 1904) but is rare in the U. Oxfordian of England where *E. spondyloides* is common. In the Kimmeridgian *E. velatus* is found sporadically in the faunally depauperate marls and limestones of Switzerland (de Loriol, 1878) and S. Germany (Staesche, 1926) where it reaches a maximum height of 75 mm (GPIT). In the L. Tithonian *E. velatus* returns to reef facies in Sicily (Gemmellaro and Di Blasi, 1874; Gemmellaro, 1875) where, however, *E. spondyloides* is a much more abundant species. In the U. Tithonian *E. velatus* appears to be common in the Stramberg coral reef (assoc. fauna p. 88) reaching a maximum height of 84 mm (Boehm, 1883; Remes, 1903).

The great majority of museum specimens are left valves and those from argillaceous horizons such as the U. Toarcian and Kimmeridgian (e. g. OUM J33475, BM unnumbered, GPIT) often show xenomorphic ornament derived from ammonites (Pl. 5, Fig. 4). Apart from those cases discussed above *E. velatus* is an infrequent species.

8. INTERPRETATION OF ECOLOGY

It is apparent from Section 7 that throughout most of its range *E. velatus* was an inhabitant of argillaceous facies. In some cases the soupy substrates characteristic of such facies seem to have been avoided by means of fixation to the hard shells of ammonites. However, far from all specimens show evidence for such a mode of life. Moreover, *E. velatus* is conspicuously rare in argillaceous deposits such as occur in the U. Jurassic of the peri-Mediterranean region and the L. Toarcian of N. Europe where ammonites are abundant but benthos is very sparse. Attachment to the living pelagic ammonite therefore seems improbable and it is more likely that some benthic element, probably bivalves, constituted the usual attachment site while dead ammonite shells resting on the sea floor provided an acceptable, if not ideal, alternative where benthos was restricted (e. g. U. Toarcian and Kimmeridgian marls and limestones). Viewed in these terms the abundance of *E. velatus* in some reefs can be seen as a response to the abundance of hard bodied benthic elements (including bivalves) providing numerous suitable attachment sites. The absence or rarity of the species in other coralliferous horizons (e. g. U. Oxfordian of England, L. Tithonian of Sicily) is correlated with the presence of numerous *E. spondyloides* and is therefore suggestive of a competitive reaction (see Section 6). There seems to be no definite correlation between facies type and the maximum size of *E. velatus*.

Irregularly shaped Recent morphological analogues of *E. velatus* include *Pedum spondyloideum*, a species which lives byssally attached deep within coral heads (Yonge, 1967; Waller, 1972b), and *Hinnites multirugosus*, a species which cements its right valve to rocks and other bivalves (Yonge, 1951).

9. FUNCTIONAL MORPHOLOGY

The extremely large byssal notch of *E. velatus* implies that byssal fixation could have been maintained throughout ontogeny. The reduced ornamentation of the right valve is adaptive for tight byssal fixation and the general irregularity of shape, occasional presence of undoubted xenomorphic ornament,and restriction of serpulid encrustation to the left valve indicates that the right valve was indeed closely applied to the substrate for long periods. The variability of shell form led many earlier authors to presume a cemented mode of life similar to that of *Hinnites*, to which genus the species was thus assigned (see Synonymy). The paucity of right valves also seems to argue for this hypothesis. However, Cox (1942) in a survey of *Eopecten* right valves, including those of *E. velatus*, was unable to find positive evidence of cementation. Moreover, A. Seilacher (pers. comm., 1977) has observed discontinuities in the pattern of xenomorphic ornament derived from ammonites which imply movement of the shell. Thus tight fixation must have been effected solely by a renewable byssus rather than by a byssus and a permanent cement. The rarity of right valves may be explained by their relative thinness and increased susceptibility to breakage.

Pedum spondyloideum and crevice-dwelling individuals of *Hinnites multirugosus* (see Section 8) show ventral migration of the hinge line as an adaptation to living in confined spaces where both valves make contact with the substrate upon gaping. This feature has not been observed in *E. velatus* so it would seem that the species did not occupy such microhabitats. Due to the considerable height attained (84 mm), it is doubtful whether *E. velatus* could have been byssally supported from above in reef facies. In the lack of evidence for crevice/fissure dwelling it would appear that the species must have attached to roughly horizontal upward-facing surfaces.

10. ORIGINS AND EVOLUTION

Since *E. velatus* is first recorded from the Planorbis zone its origins probably lie in the Trias. Staesche (1926) considered that *Chlamys dispar* (? = *Ch. (Ch.) valoniensis* q. v.) was ancestral but Dechaseaux (1936) has pointed out that the Trias species *'Pecten' Morrissii* and *'P.' Albertii* are very similar to *Eopecten* and these represent a more plausible root stock.

E. velatus apparently undergoes a phyletic increase in range and reduction in mean number of costae in the passage from L. to U. Jurassic (see Section 4). Maximum height follows an oscillatory course in the passage from L. Pliensbachian (63 mm) to U. Pliensbachian (110 mm) to Toarcian (75 mm) to Aalenian (101 mm) to Oxfordian (70 mm) to Kimmeridgian (75 mm) to Tithonian (84 mm).

Eopecten spondyloides (Roemer 1836)

Pl. 5, Figs. 9–14, Pl. 6, Figs. 2, 4, 7, ?Fig. 1; text figs. 142–144

Synonymy

1822 *Ostrea ?;* Young and Bird, pl. 10, fig. 3.
pv*? 1836 *Spondylus tuberculosus* sp. nov; Goldfuss, p. 93, pl. 105, figs. 2a, 2b.
1836 *Avicula spondyloides* sp. nov; Roemer, p. 87, pl. 13, figs. 14a, 14b.
1850 *Avicula jason* sp. nov; d'Orbigny, v. 1, p. 313 (Boule, 1912, v. 7, p. 161, pl. 2, figs. 17–19).
1850 *Avicula janthe* sp. nov; d'Orbigny, v. 1, p. 313 (Boule, 1912, v. 7, p. 162, pl. 1, figs. 47, 48).
1850 *Hinnites Psyche* sp. nov; d'Orbigny, v. 1, p. 314 (Boule, 1912, v. 7, p. 165).
v* 1850 *Hinnites Pamphilus* sp. nov; d'Orbigny, v. 1, p. 342 (Boule, 1925, v. 14, p. 161, pl. 20, fig. 14).
v* 1850 *Hinnites Paniscus* sp. nov; d'Orbigny, v. 1, p. 342 (Boule, 1925, v. 14, p. 161, pl. 20, fig. 13).
1853 *Hinnites velatus* (Goldfuss); Morris and Lycett, p. 14, pl. 2, figs. 2, 2a (non Goldfuss sp.).
1853 *Hinnites tegulatus* sp. nov; Morris and Lycett, p. 14, pl. 2, figs. 3, 3a.
1855 *Hinnites abjectus* (Phillips); Morris and Lycett, p. 125, pl. 14, fig. 3 (non Phillips sp., non pl. 9, fig. 7).
1858 *Pecten tuberculosus Gingensis* subsp. nov; Quenstedt, p. 379, pl. 51, fig. 4 (?Goldfuss sp.).
non 1858 *Pecten tuberculosus* (Goldfuss); Quenstedt, p. 434, pl. 59, figs. 9, 10.
1859 *Pecten Parisoti* sp. nov; Contejean, p. 313, pl. 23, figs. 19–21.
1862 *Hinnites velatus* (Goldfuss); Thurmann and Étallon, p. 266, pl. 37, fig. 12 (non Goldfuss sp.).
v* 1863 *Hinnites fallax* sp. nov; Dollfus, p. 85, pl. 15, fig. 14, pl. 16, figs. 9, 10.
1864 *Hinnites velatus* (Goldfuss); Dumortier, p. 70, pl. 4, figs. 1–3 (non Goldfuss sp.).
1867 *Hinnites Gingensis* (Quenstedt); Waagen, p. 633, pl. 31, figs. 1a, 1b, 2a, 2b.
1872 *Hinnites fallax* Dollfus; de Loriol et al., p. 394, pl. 23, fig. 3.
1872 *Hinnites Cornueli* sp. nov; de Loriol in de Loriol et al., p. 395, pl. 23, fig. 4.
1874 *Hinnites velatus* (Goldfuss); Dumortier, p. 195, pl. 43, fig. 6 (non Goldfuss sp.; non p. 308, pl. 62, figs. 3, 4.).
1875 *Hinnites Lorioli* sp. nov; Gemmellaro, p. 63, pl. 7, fig. 2.
1886d *Hinnites velatus* var. *irgetus* var. nov; De Gregorio, p. 20, pl. 13, figs. 1–6 (non Goldfuss sp.).
1888 *Hinnites clathratus* sp. nov; Schlippe, p. 136, pl. 2, fig. 2.
1893 *Hinnites Cornueli* de Loriol; de Loriol and Lambert, p. 145, pl. 10, figs. 10, 11.
1893 *Hinnites? spondyloides* (Roemer); de Loriol, p. 314, pl. 33, figs. 9, 10.
1893 *Hinnites? Lepidus* sp. nov; de Loriol, p. 316, pl. 33, figs. 11, 12.
1898 *Pecten (Velopecten) Sarthensis* sp. nov; E. Philippi, p. 602, pl. 19, fig. 1.
1905 *Hinnites Cornueli* de Loriol; Peron, p. 239, pl. 10, fig. 11.
1905 *Hinnites* cf. *spondyloides* (Roemer); Peron, p. 240, pl. 10, fig. 12.
1906 *Eopecten tegulata* (Morris and Lycett); Cossmann, p. 2, pl. 1, figs. 3–5.
1912 *Eopecten Psyche* (d'Orbigny); Dal Piaz, p. 247, pl. 2, figs. 1a, 1b.
1915 *Hinnites (Prospondylus) Ernii* sp. nov; Rollier, pp. 448, 465, pl. 30, figs. 1–4.
1915 *Hinnites (Prospondylus) oolithicus* sp. nov; Rollier, p. 455.
1915 *Hinnites (Prospondylus) Morrisi* sp. nov; Rollier, p. 455.
1915 *Hinnites (Prospondylus) Peroni* sp. nov; Rollier, p. 460.
1915 *Hinnites (Prospondylus) astartinus* sp. nov; Rollier, p. 462.
1915 *Hinnites (Prospondylus) Aeberhardti* sp. nov; Rollier, p. 447, pl. 29, figs. 3, 4.
1923 *Pecten (Velata)* sp. nov; Ernst, p. 60, pl. 1, fig. 12.
1923 *Eopecten tuberculosus* (Goldfuss); Lissajous, p. 157 (? Goldfuss sp.).
1926 *Velopecten Gingensis* (Quenstedt); Staesche, p. 120.
v 1926 *Velopecten Jason* (d'Orbigny); Staesche, p. 121, pl. 5, fig. 3, pl. 6, fig. 12.
v 1926 *Velopecten spondyloides* (Roemer); Staesche, p. 124, pl. 6, fig. 10.
1926 *Velopecten velatus* (Goldfuss); Arkell, p. 549, pl. 34, fig. 6 (non Goldfuss sp.).
v* 1931a *Velata anglica* sp. nov; Arkell, p. 120, pl. 9, figs. 1, 1a, 2.
1931a *Velata wiltoniensis* sp. nov; Arkell, p. 123, pl. 9, figs. 3, 3a.
non 1936 *Velata tuberculosa* (Goldfuss); Dechaseaux, p. 68, pl. 9, fig. 2.
1936 *Velata Gingensis* (Quenstedt); Dechaseaux, p. 68.
1936 *Velata Cornueli* (de Loriol); Dechaseaux, p. 70.
1936 *Velata fallax* (Dollfus); Dechaseaux, p. 71.
1948 *Velata tegulata* (Morris and Lycett); Cox and Arkell, p. 15.
1952 *Eopecten tegulatus* (Morris and Lycett); Cox, p. 29, pl. 3, figs. 5–7.

The type material of *Avicula spondyloides* Roemer, 1836, p. 87, pl. 13, figs. 14a, 14b is probably in the Roemer-Pelizaeus-Museum, Hildesheim, W. Germany. It was derived from the Oxfordian of N. Germany.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

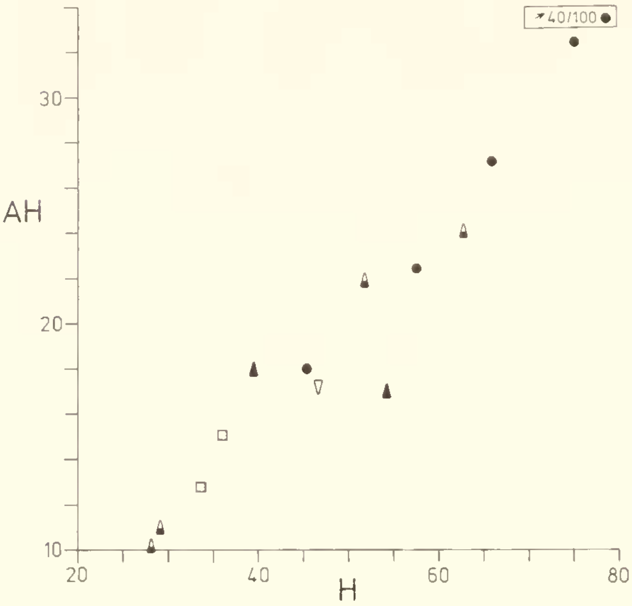
'*A.* valva dextra oblique ovato-orbiculari fornicata 20–30 costulata, ala antica obsoleta postica depressa permagna costulata, costulis subnodulosis, sulcis interstitialibus linea ornatis.

Die allein vorliegende rechte Schale ist breit-eirund, fast kreisrund, hoch gewölbt und hinten durch starke Niederbiegung in einen großen Flügel übergehend. Die ganze Oberfläche ist mit 20 bis 30 scharfen, etwas knötigen Rippen bedeckt, in deren Zwischenräumen man eine deutliche Längslinie bemerkt. Der etwas zugespitzte Buckel liegt ziemlich in der Mitte.

Findet sich 12 bis 18 Linien groß im unteren Coral rag bei Heersum und im mittleren Coral Rag bei Hannover. Die Gattungskennzeichen haben noch nicht genau untersucht werden können.'

2. AMENDED DIAGNOSIS

Distingusihed from *E. velatus* by the tendency, on the left valve, for intercalary costae to rapidly gain the same height as originals. Distinguished from *E. abjectus* by the similarity in height of the original costae.



Text fig. 142: *Eopecten spondyloides* – anterior hinge length/height.

3. AMENDED DESCRIPTION

Essentially very similar to *E. velatus* in its often irregular shape (e. g. Pl. 5, Fig. 10) and variable H/L and AH/H (text figs. 143, 142). The main difference lies in the radial ornament of the left valve which consists of about 20 original costae which are continually added to by the intercalation of new costae (rapidly gaining the same height as originals) such that at H: 10 there are between 22 (OUM J34325) and 32 (YM 679) costae, at H: 20 between 30 (OUM J34325) and 48 (YM 679) costae, at H: 30 between 40 (YM 442) and 56 (OUM J34325) costae, at H: 50–60 over 100 costae (Arkell, 1931a) and so on. The left valve of *E. spondyloides* also exhibits small, closely spaced imbricate lamellae on the costae unlike the left valve of *E. velatus* which bears only growth lines in addition to the costae.

The maximum height of *E. spondyloides* is 140 mm (Waagen, 1867).

4. DISCUSSION

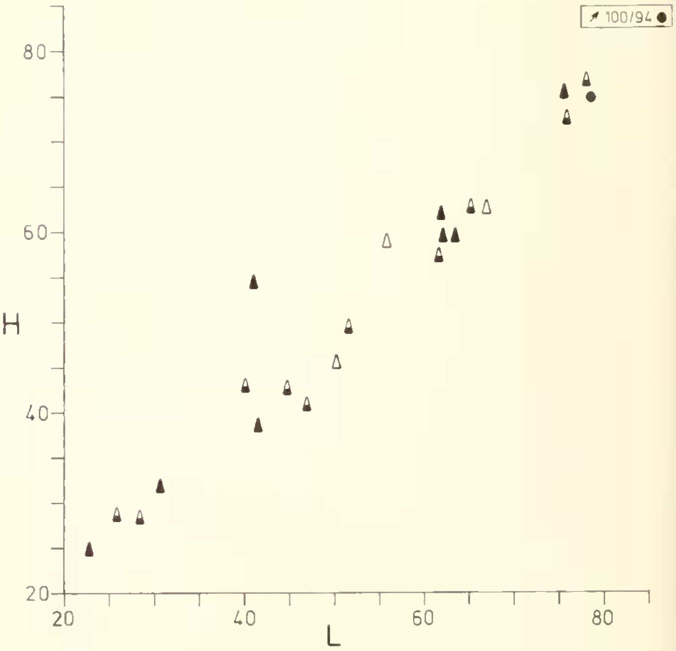
As in *E. velatus* the extreme variability in shape and ornament of the species described in Section 3 has resulted in the proliferation of a vast number of specific names, in many cases based on a very small number of specimens. Those species which are, in the author's opinion, adequately characterised (by means of available types, clear illustrations or detailed descriptions) such that there can be no doubt as to their affinity with the species described in Section 3, are placed in synonymy but not discussed, it being deemed of little value to attempt to describe individual variants. Secondary references to these species are only included in the synonymy where there can be no doubt as to their systematic position. Equivocal secondary references may be traced in Terquem and Jourdy (1869), de Loriol and Pellat (1875), Siemiradzki (1893), Cossmann (1900, 1907a, 1914, 1922), Paris and Richardson (1916), Lissajous (1923), Lanquine (1929), Dechaseaux (1936), J.-C. Fischer (1964) and Behmel and Geyer (1966).

Although the author has been unable to examine the holotype (M) of *'Avicula' spondyloides* Roemer there can be little doubt from the illustration that it is an example of the species described in Section 3. The holotype (M) of *Spondylus tuberculosus* Goldfuss (BSPHG AS VII 640; Pl. 6, Fig. 1), a species erected in the same year as Roemer's, shows some resemblance to the species described in Section 3 but its rather coarse ornament and high convexity suggest that it is in fact an example of *Eopecten abjectus*. As the earliest specific name erected for an undoubted example of the species described above, *'A.' spondyloides* is herein taken to be the senior synonym.

Quenstedt (1858; *'Pecten' tuberculosus Gingensis* only) and Lissajous (1923) have used Goldfuss' specific name for examples of *Eopecten spondyloides*; *'Pecten' tuberculosus* (Goldfuss); Quenstedt is representative of *E. abjectus* while *'Velata' tuberculosa* (Goldfuss); Dechaseaux is apparently an example of *Ctenostreon*.

The frequent misapplication of the name *velatus* Goldfuss to *E. spondyloides* (see Synonymy) is discussed under *E. velatus* and Morris and Lycett's (1853) incorrect use of *'Hinnites' abjectus* (Phillips) is discussed under *E. abjectus*.

'H.' ('Prospondylus') astartinus Rollier should be rejected as a junior secondary homonym of *'H.' astartinus* Greppin (= *E. velatus*).



Text fig. 143: *Eopecten spondyloides* – height/length.

Although unfigured and inadequately described, Rollier's (1915) species *'H.' ('Pr.') oolithicus*, *'H.' ('Pr.') Morrisi*, *'H.' ('Pr.') Peroni* and *'H.' ('Pr.') astartinus* are based on specimens figured in respectively Morris and Lycett (1853, 1855), Peron (1905) and de Loriol and Lambert (1893) which are clearly referable to *E. spondyloides*.

5. STRATIGRAPHIC RANGE

Two rather poor specimens from the Sinemurian of Belgium (BM LL8605, LL8606) may be early representatives of *E. spondyloides*. The first certain records are however from the L. Toarcian when the species is recorded rarely from the Rhone basin (Dumortier, 1874). De Gregorio's (1886d) record from N. Haly may be from a similar horizon. U. Toarcian records are limited to a single specimen from N. W. Germany (Ernst, 1923) but in the Aalenian a number of specimens are known from France and England. *E. spondyloides* is quite common in the Bajocian and Bathonian but the only records from the Callovian are two specimens from France (MNO 3402B, 3403) and seven from N. W. India (Cox, 1952). The species becomes common again in the Oxfordian but Kimmeridgian reports, although widespread, seem, where abundances are known, to be of very small numbers of specimens, e. g. in France, two from Le Havre (BM LL13478; ENSM L336, Pl. 6, Fig. 2), one from Montbéliard (Contejean, 1859) and one from La Rochelle (N. J. Morris Collection, BM). The species is reported to be common in the L. Tithonian of Sicily (Gemmellaro, 1875) and is known from the Tithonian of S. Germany (Staesche, 1926) and Stramberg in Czechoslovakia (BM LL23888; Pl. 6, Fig. 4).

6. GEOGRAPHIC RANGE

E. spondyloides occurs widely in Europe (text fig. 144). Outside Europe, the only record is from the Callovian of N. W. India (see Section 5). This occurrence, matched with the rarity of the species in the Callovian of Europe, may signify an emigration, perhaps because of the widespread development of unfavourable argillaceous facies (see Section 8).

7. DESCRIPTION OF ECOLOGY

Although fairly widespread in the Aalenian *E. spondyloides* is notably rare in the chamositic oolites of the Northampton Sand Ironstone, in which *E. abjectus* frequently occurs. Only three specimens (BM 82394, L25732, unnumbered; the first attaining a height of 63 mm) are known from this horizon.

E. spondyloides is found at most levels in the Bajocian but is most common in the L. Bajocian Lincolnshire Limestone and the Sowerbyi-Banke of S. W. Germany (Staesche, 1926), where it reaches a maximum height of 140 mm (Waagen, 1867). The sediments in the latter case are condensed marly oolites containing few ammonites but a diverse benthic fauna, mainly consisting of bivalves (including occasional examples of *E. abjectus*).

Many levels were colonised in the Bathonian (Cox and Arkell, 1948) but the species seems to be commonest in the L. Bathonian Minchinhampton Beds, grain supported oolites containing a diverse bivalve and gastropod fauna but very few ammonites (Morris and Lycett, 1851–55). The maximum height attained is 49 mm (BM LL847). Two specimens (BM 65909, 65913) are known from coral containing beds (Couches à Polypiers) in the Bathonian of Normandy.

In the Oxfordian *E. spondyloides* is quite common at most horizons and reaches a maximum height of 116 mm (OUM J8255). The author has collected numerous examples (reaching a maximum height of about 75 mm) from the Coral Rag (Transversarium zone) of Whitewall Corner Quarry near Malton, Yorkshire, where the species occurs in a tough porcellanous limestone crowded with corals *(Thamnasteria, Rhabdophyllia, Thecosmilia* and *Stylina)* and a reef-derived fauna including *Ctenostreon*, *Lithophaga* and the 'coarse' phenotype of *Chlamys (Ch.) textoria* together with the regular echinoid *Cidaris* (J. Wright, 1972). *E. velatus* is unknown. Similar facies characterise occurrences in the Unterer Korallenoolith (Plicatilis zone) of N. W. Germany (Roemer, 1836) and the Ringstead Coral Bed (Pseudocordata zone) in Dorset (BM 73077). However, in coral reef facies in the

Text fig. 144: *Eopecten spondyloides* – European distribution.

U. Oxfordian of the Yonne where *E. velatus* is common, *E. spondyloides* appears to be rare.

In the Kimmeridgian the maximum height of 92 mm (ENSM L336) is attained in clay facies (Dollfus, 1863). However, the majority of reports seem to be from coralliferous deposits, e. g. the Tafel Jura (Contejean, 1859), Haute-Marne (de Loriol et al., 1872) and Charente Maritime (N. J. Morris Collection, BM).

In reefal limestones in the L. Tithonian of Sicily (fauna p. 88) *E. spondyloides* is reported to be very common, reaching a maximum height of 71 mm, while *E. velatus* appears to be comparatively rare (Gemmellaro, 1875). In similar facies in the U. Tithonian at Stramberg *E. velatus* seems to be common but only one definite specimen of *E. spondyloides* is known (BM LL23888; H: 46.5). Stafsche (1926) records the species from oolites (Brenztaloolith) of the same age in S. Germany which pass laterally into coral/*Diceras* facies (Arkell, 1956).

E. spondyloides is rare in argillaceous deposits at all times. Only two specimens (BM LL13478, ENSM L336) are known from the Kimmeridge Clay and two from the Oxford Clay (SM J26440, J6441). Dumortier (1874) records only rare specimens from L. Toarcian clays in the Rhone. Of these a high proportion are said to bear xenomorphic ornament derived from ammonites. The only records from the M. and U. Jurassic of the peri-Mediterranean area, where sedimentation was predominantly pelagic, are from N. Italy (De Gregorio, 1886d, Dal Piaz, 1912) where a guyot was probably in existence.

The great majority of museum specimens of *E. spondyloides* are left valves.

8. INTERPRETATION OF ECOLOGY

The usual occurrence of *E. spondyloides* in oolitic and reefal limestones indicates a preference for high energy conditions. Absence of the species from L. Bajocian reefs in the E. Paris Basin (Hallam, 1975b), presence of a few specimens in Bathonian coralliferous deposits and relative abundance in U. Jurassic coral reefs suggests an evolutionary change in the favoured habitat from level bottom oolites to upstanding reefs. In this connection it should, however, be noted that *Spondylopecten* species, which are frequently reef-associated, are absent from the L. Bajocian structures and this may indicate that the lack of *E. spondyloides* is due to some unfavourable feature of these reefs (e. g. dense structure, see p. 89) rather than a preference for contemporaneous oolites. Furthermore, the widespread occurrence of *E. spondyloides* in the Oxfordian of England and the typically small size and localised distribution of coral reefs suggests that at least some records bear no relation to the existence of reefs. Moreover, the virtual restriction of the species to reef and reef-derived sediments in the U. Jurassic of continental Europe may simply be a result of the general development of unfavourable low energy, argillaceous facies elsewhere. Epifaunal bivalves probably afforded suitable attachment sites in level bottom environments and the abundance of *E. spondyloides* in reefs could be more a consequence of the abundance of bivalves rather than of a direct relationship with corals. The evolutionary trend suggested above may therefore be more apparent than real.

Although a high proportion of the relatively few examples of *E. spondyloides* from the L. Toarcian of the Rhone show evidence of having been attached to ammonites, the abundance of the species in deposits in which ammonites are rare and the fact that only two other specimens (YM 442 from the Inferior Oolite of Dorset, GPIT from the Bajocian/Bathonian of S. Germany) with ammonite-derived xenomorphic ornament are known, indicates that ammonites did not provide ideal attachment sites but constituted a considerably less favourable alternative to bivalves. By analogy with *E. velatus* it is probable that ammonites were only used for attachment when they had sunk to the sea floor after death.

The inverse relationship between the numbers of *E. spondyloides* and *E. velatus* in U. Jurassic reefs is good evidence for competition. The dominent species at any one locality was presumably determined by priority. A similar reaction seems to have occurred between *E. spondyloides* and *E. abjectus* in M. Jurassic oolites.

There is no obvious relationship between size and facies in *E. spondyloides*. Its usual occurrence, in moderate numbers with a high diversity fauna, suggests that it was an equilibrium species (Levinton, 1970).

9. FUNCTIONAL MORPHOLOGY

Since in all important morphological respects *E. spondyloides* is identical to *E. velatus* the interpretation of functional morphology offered for the latter will serve here.

10. ORIGINS AND EVOLUTION

The most likely ancestor for *E. spondyloides* is *E. velatus*. A large (H: 75) specimen of the latter (Pl. 5, Fig. 8) exhibits, in late ontogeny, ornament which closely resembles that of the early ontogeny of *E. spondyloides*. Thus trans-specific evolution could have occurred by the relatively 'simple' process (Gould, 1977) of the acceleration (recapitulation) of the development of ornament with respect to size.

There are no directional changes in morphology within *E. spondyloides*. Maximum height oscillates from 63 mm (Aalenian) to 140 mm (Bajocian) to 49 mm (Bathonian) to 55 mm (Callovian, Macrocephalus zone; Cox, 1952) to 116 mm (Oxfordian) to 92 mm (Kimmeridgian) to 71 mm (Tithonian). The Callovian value is derived from a rather small sample so it is likely that the maximum height recorded in the stage will be increased on further collecting.

Eopecten abjectus (Phillips 1829)

Pl. 6, Figs. 3, 5, 6, 8, 9, ?Fig. 1; text fig. 145

Synonymy

1829	*Pecten abjectus* sp. nov; Phillips, pl. 9, fig. 37.
1835	*Pecten abjectus* Phillips; Phillips, pl. 9, fig. 37.
pv*? 1836	*Spondylus tuberculosus* sp. nov; Goldfuss, p. 93, pl. 105, figs. 2a, 2b.
1855	*Hinnites abjectus* (Phillips); Morris and Lycett, p. 125, pl. 9, fig. 7 (non pl. 14, fig. 3).
non 1858	*Pecten tuberculosus Gingensis* subsp. nov; Quenstedt, p. 379, pl. 51, fig. 4 (?Goldfuss sp.).

v 1858 *Pecten tuberculosus* (Goldfuss); Quenstedt, p. 434, pl. 59, figs. 9, 10.
1863 *Hinnites gradus* sp. nov; Bean in Lycett, p. 35, pl. 33, figs. 10, 10a.
1883 *Hinnites abjectus* (Phillips); de Loriol and Schardt, p. 72, pl. 10, figs. 12, 13.
1910 *Eopecten gradus* (Bean); Lissajous, p. 351.
1910 *Eopecten abjectus* (Phillips); Lissajous, p. 351, pl. 9, fig. 14.
1916 *Eopecten abjectus* (Phillips); Paris and Richardson, p. 530.
1923 *Eopecten Gradus* (Bean); Lissajous, p. 157.
non 1923 *Eopecten tuberculosus* (Goldfuss); Lissajous, p. 157 (?Goldfuss sp.).
1926 *Velopecten abjectus* (Phillips); Staesche, p. 119.
1936 *Velata abjecta* (Phillips); Dechaseaux, p. 68.
1936 *Velata gradus* (Bean); Dechaseaux, p. 69.
1948 *Velata gradus* (Bean); Cox and Arkell, p. 15.

No trace of the type material of *Pecten abjectus* Phillips 1829, pl. 9, fig. 37 has yet been found despite considerable searching in e. g. the Phillips Collections at OUM and YM. The figured specimen was said by Phillips to be from the Yorkshire Gt. Oolite (Bathonian). This seems unlikely in view of the non-marine facies; a Bajocian or Aalenian age is more probable.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

None given.

2. DIAGNOSIS

Distinguished from *E. spondyloides* by the tendency for two median costae to be considerably larger and bear tubercles. Distinguished from *E. velatus* by the tendency for intercalary costae to rapidly gain the same height as original costae.

3. DESCRIPTION

Essentially very similar to *E. spondyloides* apart from the diagnostic features. The number of costae on the left valve is however usually much smaller (e. g. 40 at H: 53.5, OUM J2291) at equivalent size, and convexity, although very variable, is usually much higher (C_L: 21.5 at H: 58, BM 70686). The maximum height is 127.5 mm (GPIT).

4. DISCUSSION

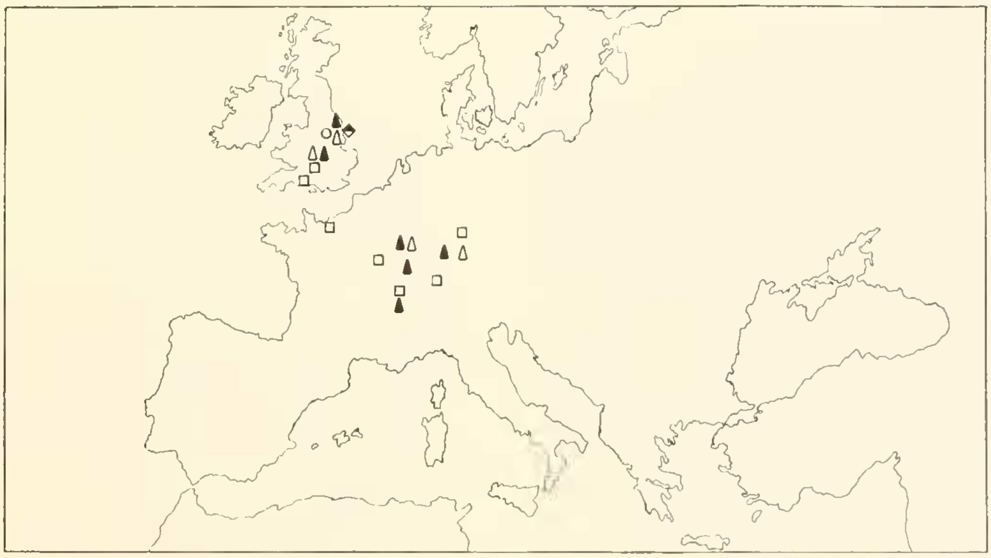
Phillips' (1829) figure of '*Pecten*' *abjectus* in the first edition of Geology of Yorkshire is a poor illustration of a coarsely ornamented *Eopecten*. There is little sign of the larger tubercle-bearing costae diagnostic of the species described in Section 3. The figure in the second edition (1835), while undoubtedly of the same specimen, is considerably clearer and yields a costal count of 36 at H: 37. This is a reasonable value for the species described in Section 3 and well below the lower limit of variation in *E. spondyloides*, the only species with which there is any possibility of confusion. The original specimen seems to have been lost (see above) but in the light of the above evidence it can be assumed to have been a variant of the species described in Section 3 with relatively undeveloped median costae. The majority of subsequent usage of Phillips' specific name (see Synonymy) has been for representatives of the species described in Section 3 thus there would be good grounds for designating as neotype a typical example of this species.

One of the figures (pl. 14, fig. 3) of '*H.*' *abjectus* in Morris and Lycett (1855) depicts a specimen with the more numerous and regular costae characteristic of *E. spondyloides*.

Lissajous (1910) states that the specific name *gradus* Bean dates from the latter's paper in Ann. Mag. Nat. Hist. (1839). However, there is no reference to the species in this paper and the earliest reference to it would therefore appear to be in Lycett (1863), where a specimen which clearly belongs to *E. abjectus*, is described and figured as '*P.*' *gradus* Bean.

'*Spondylus*' *tuberculosus* Goldfuss and secondary usages of this specific name are discussed under *E. spondyloides*.

Inadequately characterised secondary references to synonymous species are excluded from the synonymy because of the possibility of misapplication to *E. spondyloides*.



Text fig. 145: *Eopecten abjectus* – European distribution.

They may be traced in Oppel (1858), Rothpletz (1886), Schlippe (1888), Kilian and Guébhard (1905), Hennig (1924), Lanquine (1929), Parent (1940), Channon (1950) and J.-C. Fischer (1969).

5. STRATIGRAPHIC RANGE

A single specimen from the U. Pliensbachian of Yorkshire (BM 47353; Pl. 6, Fig. 9) is the earliest record of *E. abjectus*. Thereafter the species is unknown until the Aalenian when it becomes locally quite common, continuing thus until the U. Bajocian. Unequivocal Bathonian records (Morris and Lycett, 1855; de Loriol and Schardt, 1883; Lissajous, 1923; Staesche, 1926; Dechaseaux, 1936; Cox and Arkell, 1948) are fairly widespread in Europe but the species does not appear to be common anywhere. Callovian records are limited to a single specimen from the Macrocephalus zone of Scarborough (Lycett, 1863) and unfigured and therefore questionable specimens (see Section 4) from the Maritime Alps (Kilian and Guébhard, 1905). Morris and Lycett's (1855) record from the 'Coralline Oolite of Malton' (Oxfordian) is unsupported by a figure of a specimen from this horizon.

6. GEOGRAPHIC RANGE

The distribution of *E. abjectus* in Europe (text fig. 145) is largely dependent on the occurrence of the appropriate sedimentary facies (see Section 8). The only records from outside Europe are a single specimen from the U. Bathonian of N. W. India (BM L75269) and unfigured and therefore questionable specimens (see Section 4) from the 'Lower Dogger' of Tanzania (Hennig, 1924).

7. DESCRIPTION OF ECOLOGY

E. abjectus first occurs commonly in the Northampton Sand Ironstone (Opalinum zone), a condensed chamosite oolite containing few examples of *E. spondyloides* but an otherwise abundant and diverse fauna. The maximum height attained is 95 mm (BM 82385). *E. abjectus* is markedly less common in the Sowerbyi-Banke, a somewhat similar condensed, ferruginous, marly oolite containing numerous examples of *E. spondyloides*, in the L. Bajocian of S. W. Germany. Maximum height (127.5 mm, GPIT) is however considerably greater.

Lissajous (1923) reports the species to be common in ferruginous oolites of the Parkinsoni zone (U. Bajocian) in the Mâconnais. *E. spondyloides* appears only to occur in the Toarcian and Bathonian in the same area. In the U. Bajocian of Swabia *E. abjectus* reaches a maximum height of 75 mm (GPIT).

It is clear from the foregoing that condensed ferruginous oolites constituted the most favourable substrate for *E. abjectus*. The species is not known to be common outside this facies. Paris and Richardson (1916) report the species to be common in the Pea Grit (Murchisonae zone), a pisomicrite in the Cotswolds, but this is not reflected in museum collections or supported by the present author's field observations.

8. INTERPRETATION OF ECOLOGY

The usual occurrence of *E. abjectus*, in condensed ferruginous oolites, indicates a preference for high energy conditions with minimal terrigenous input. The inverse correlation in numbers of *E. abjectus* and *E. spondyloides* in such facies is strongly suggestive of competition, with dominance at any one locality being presumably determined by priority.

The characteristic field occurrence of *E. abjectus*, in moderate numbers with a high diversity fauna, suggests that it was an equilibrium species (Levinton, 1970).

9. FUNCTIONAL MORPHOLOGY

Since the species are in all important respects identical, the interpretation of functional morphology presented for *E. velatus* is of equal relevance to *E. abjectus*. It is extremely doubtful whether the coarser ornament of the latter conferred any useful additional strength and stiffness on the shell which, being thick, must already have been robust enough to cope with most eventualities. The coarser ornament is more probably a non-functional by-product of neoteny in the origin of the species (see Section 10).

No specimens of *E. abjectus* bearing the xenomorphic ornament of ammonites have been discovered. It therefore seems likely that benthos provided the sole source of sites for byssal attachment.

10. ORIGIN AND EVOLUTION

On the basis of morphology the most likely ancestor for *E. abjectus* is *E. spondyloides*. However, validation of this hypothesis of derivation must await the discovery of undoubted specimens of *E. spondyloides* from the L. Lias (see Section 5). Since the relatively coarse ornament of *E. abjectus* resembles the juvenile ornament of *E. spondyloides* it is possible that trans-specific evolution involved the retardation of ornamental development with respect to size (neoteny). There is however no basis of allometry in *E. spondyloides* to allow derivation of the large tuberculate median costae in *E. abjectus* by heterochrony. Speciation therefore probably involved changes in the structural as well as the regulatory genome.

There appear to be no phyletic changes in morphology within *E. abjectus*. Maximum height shows no directional change in the passage from Aalenian (95 mm) to L. Bajocian (127.5 mm) to 75 mm (U. Bajocian).

A possibility of neoteny in the origin of *E. abjectus* together with the subsequent highly developed stenotopy is indicative of the prevalence of 'K' selection (Gould, 1977).

The Bathonian decline of *E. abjectus* was probably the result of the diminution in areal importance of ferruginous oolite deposits. The subsequent extinction of the species in the Callovian was probably due to the widespread development of unfavourable (low energy/high turbidity) argillaceous facies in Europe.

Genus *CHLAMYS* Röding 1798 (non Koch 1801)

Type species. SD; Herrmannsen 1847, p. 231; *Pecten islandicus* Müller 1776, p. 248; Recent, circumboreal.

AMENDED DIAGNOSIS

'Higher than long or rounded, commonly somewhat oblique, LV usually more convex but in some species valves nearly equally convex; auricles clearly delimited, usually large; byssal notch large; ctenolium usually present; sculpture of radial (usually stronger) and concentric elements, with scalelike spines commonly developed at their junctions, especially on LV but some shells nearly smooth; interspaces of many forms with intercalaries in adult; margin usually scalloped; cardinal crura variable in number and size. Trias. – Rec., cosmop.' (Hertlein, 1969: N355).

DISCUSSION

The above diagnosis includes such a diversity of forms that it seems impractical to employ it at the generic level. However, the present author is not in a position to give a revised generic diagnosis of *Chlamys* since most species are post-Jurassic.

Subgenus *CHLAMYS* s. s.

(Synonyms etc. *Clamys* Leach, 1815 [nom. null.]
Chalmys Dollfus and Dautzenberg, 1886 [nom. null.]
Actinochlamys Rovereto, 1898
Myochlamys von Ihering, 1907 [obj.]
Chlamydina Cossmann, 1907 [obj.]
Zygochlamys von Ihering, 1907
Belchlamys Iredale, 1929
Mimachlamys Iredale, 1929
Scaeochlamys Iredale, 1929
Talochlamys Iredale, 1929
Veprichlamys Iredale, 1929
Coralichlamys Iredale, 1939)

AMENDED DIAGNOSIS

'Usually higher than long, anterior auricle longer than posterior one; sculpture of numerous, generally grooved or striated and spinose, radial ribs; inner margin commonly with rounded, grooved, weak riblets; cardinal crura weak or nearly obsolete. Trias. – Rec., cosmop.' (Hertlein, 1969: N355).

DISCUSSION

Forms referable herein to *Ch. (Chlamys)* are divisible into 3 groups on the following basis: –

1. Plicae smooth (= *Ch. (Ch.) valoniensis*).
2. Plicae bearing widely spaced spines up to 5 mm in length (= *Ch. (Ch.) pollux*).
3. Plicae bearing variably spaced imbricate lamellae (= *Ch. (Ch.) textoria*).

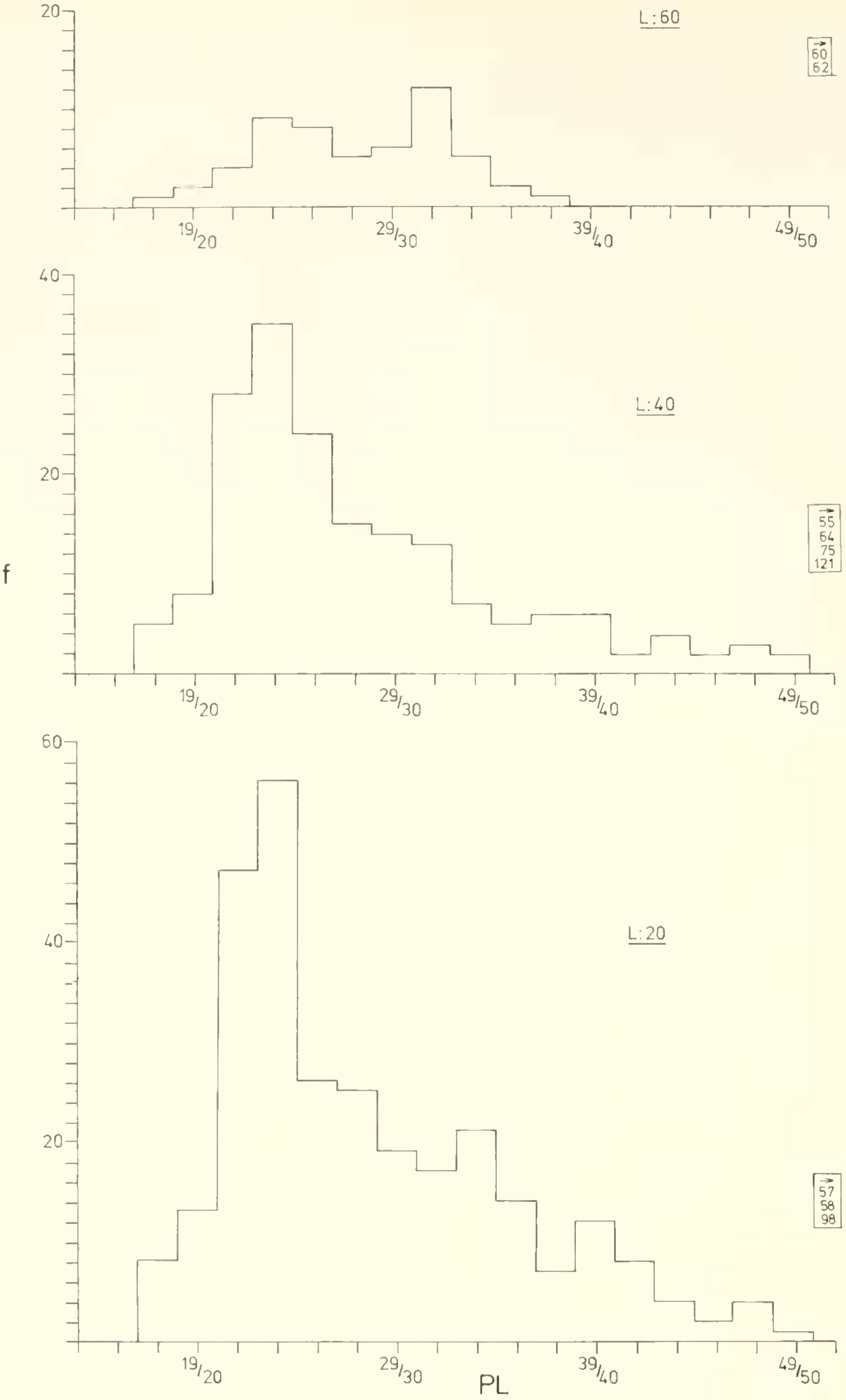
Groups 1 and 2 are almost certainly directly related and can be distinguished from Group 3 at least as far back as the Trias. They may therefore be worthy of a subgeneric distinction from Group 3. However, in view of the uncertainty over the bounds of the genus *Chlamys* (see above) this seems an inopportune moment to risk further confusion of the taxonomy by erecting new subgenera.

Forms referable to Group 3 are to all intents and purposes continuously variable in the number of plicae, spacing of the comarginal lamellae and umbonal angle (Pl. 6, Figs. 10–12, Pl. 7, Figs. 1–23, Pl. 8, Figs. 1–3, 5–20). In all other respects they are relatively invariant. However variation, at least in the number of plicae, is not normally distributed. Plical frequency histograms standardised for size (in order to eliminate the effect of ontogenetic increase in the number of plicae) show at L: 20 and L: 40 (text fig. 146) a pronounced skew to the right together with the development of secondary modes, while at L: 60 (text fig. 146) there is marked bimodality. At all sizes there are a few specimens whose plical frequencies are outside the range of continuous variation. This is hardly the pattern of variation expected of a single species but the following discussion is intended to show that it need not necessarily imply that more are present. In any case the height of the inter-modal troughs would make for difficulty in defining the boundaries between constituent species.

If a species is 'environmentally variable' (developmentally flexible) character/frequency plots for early stages in ontogeny would be expected to lack prominent modes since at this stage the organisms concerned cannot have 'experienced' the environment and started to develop the appropriate morphology (Johnson, 1981). For any given environment a single, prominent mode will emerge as development proceeds. However, if more than one environment is involved a whole variety of character/frequency distributions is possible for later stages in ontogeny (such as are represented in text fig. 146): differences in the extent of representation of particular environments, resulting from uneven sampling, will determine the shape of the character/frequency distribution.

In the group under discussion there is a considerable correlation between plical frequency in the later stages of ontogeny and the environment occupied. Forms within the range 17–26 plicae are usually derived from reefal or peri-reefal deposits while those within the range 27–36 plicae are most frequent in non-reef, shallow water facies and those with more than 36 plicae are usually derived from argillaceous sediments (see pp. 175–177). Due to abrasion, it is often difficult to count the number of plicae in the umbonal region (earliest ontogenetic stages). There does seem in fact to be a mode at about 22 plicae (range: 17–30) but there is nevertheless little sign of the multiple modes evident in counts from later ontogenetic stages. There are thus reasonable grounds for considering that differences in the number of plicae late in ontogeny are a reflection of ecophenotypic variation within a single species. There is still a need for further detailed work on early ontogenetic variation in order to substantiate the 'single species' hypothesis. An analysis of ontogenetic changes in variation along the lines employed for *Radulopecten vagans* (Johnson, 1981) would provide a test for ecophenotypic variation.

In conclusion, the curious patterns of variation shown by text fig. 146 are herein considered to be an artefact of the museum collections studied. In these, specimens derived from reefal and peri-reefal facies are much the most abundant

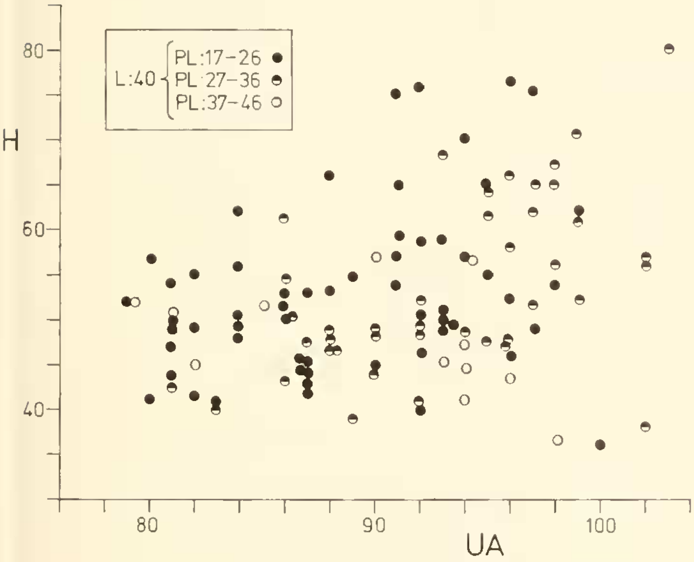


Text fig. 146: *Chlamys (Ch.) textoria* – frequency distributions for numbers of plicae at lengths of 20, 40 and 60 mm.

and thus contribute to the right-skew at L: 20 and L: 40. Specimens from argillaceous facies are poorly represented and usually small, thus resulting in the discontinuous distribution at high plical counts, which becomes especially marked at L: 60. Specimens from non-reef shallow water facies are poorly represented but often large, thus resulting in the paucity of specimens with intermediate plical counts at L: 20 and L: 40 but the relative abundance at L: 60.

Variation in the number of plicae at a particular size could result from flexibility in the absolute rate of either size increase or of addition to the number of plicae. Some evidence for retardation of size increase (stunting) is derived from the fact that forms with more than 36 plicae rarely exceed 50 mm in height. The generally closer spacing of the imbricate lamellae in such forms is also indicative of size retardation, provided that the temporal periodicity of secretion is the same as in larger specimens. Likewise, the generally smaller H/UA ratio of specimens with numerous plicae is indicative of retarded size development, provided that H and UA are partially dissociated. However, the existence of specimens which are both large and bear numerous plicae (e. g. Pl. 8, Fig. 19) should be noted. Moreover, there is by no means a linear relationship between the number of plicae and spacing of the imbricate lamellae, morphs of intermediate plical count exhibiting both close and widely spaced lamellae (e. g. Pl. 8, Figs. 9, 12). Similarly, in a plot of H/UA (text fig. 147) morphs with between 27 and 36 plicae at a standard size (L: 40) do not occupy a clearly defined zone between those with more and less plicae.

The existence of forms with low plical counts, even at very large size (e. g. Pl. 6, Fig. 12), together with the fact that much of the intercalation leading to high plical counts takes place quite early in ontogeny (e. g. Pl. 8, Fig. 16) suggests that changes in the absolute rate of addition to the number of plicae have played at least as important a role as stunting in promoting the observed pattern of ecophenotypic variation. Such changes, unlike stunting, imply some adaptive value for the phenotypes adopted in each environment. At present only a few suggestions (see p. 178) can be offered as to their significance and the topic is clearly ripe for further research.



Text fig. 147: *Chlamys (Ch.) textoria* – height/umbonal angle for forms with either 17–26, 27–36 or 37–46 plicae at a length of 40 mm.

The decision to incorporate the great range of variation of Group 3 within the bounds of a single species is not rendered suspect by the lack of a Recent analogue. In one of the few cases where the variation of a Recent pectinid has been assessed in a number of ecological settings, Beu(1966) reports that *Ch. dieffenbachi* adopts an ecophenotype consisting of numerous spine-bearing plicae when enclosed within a sponge (the usual habitat) while an ecophenotype consisting of relatively few, smooth plicae is adopted in the unenclosed condition. The total range of variation in the later stages of ontogeny is comparable to that in Group 3 and the early stages of ontogeny are similarly relatively invariant.

Chlamys (Chlamys) textoria (Schlotheim 1820)

Pl. 6, Figs. 10–12, Pl. 7, Figs. 1–21, Pl. 8, Figs. 1–3, 5–20, ?Fig. 4; text figs. 146–157

Synonymy

v* 1820 *Pectinites textorius* sp. nov; Schlotheim, p. 229.
1822 *Pecten varius* Linnaeus; Young and Bird, p. 223, pl. 9, fig. 9 (non Linnaeus sp.).
v* 1826a *Pecten vimineus* sp. nov; J. de C. Sowerby, p. 81, pl. 543, figs. 1, 2.
1828 *Pecten elegans* sp. nov; Young and Bird, p. 234, pl. 9, fig. 8.
1829 *Pecten virguliferus* sp. nov; Phillips, pl. 11, fig. 20.
? 1833 *Pecten textilis* sp. nov; Münster in Goldfuss, p. 43, pl. 89, figs. 3a–d.
v 1833 *Pecten vimineus* J. de C. Sowerby; Goldfuss, p. 44, pl. 89, figs. 7a, 7b.
v 1833 *Pecten textorius* (Schlotheim); Goldfuss, p. 45, pl. 89, figs. 9a–d.
?v* 1833 *Pecten texturatus* sp. nov; Münster in Goldfuss, p. 45, pl. 90, fig. 1.
v* 1833 *Pecten ambiguus* sp. nov; Münster in Goldfuss, p. 46, pl. 90, figs. 5a, 5b.
v 1833 *Pecten articulatus* (Schlotheim); Goldfuss, p. 47, pl. 90, fig. 10 (non Schlotheim sp.).
v* 1833 *Pecten subtextorius* sp. nov; Münster in Goldfuss, p. 48, pl. 90, figs. 11a, 11b.
1836 *Pecten subimbricatus* sp. nov; Roemer, p. 212, pl. 13, fig. 6.
1837 *Pecten textorius* var. *orbicularis* var. nov; Koch and Dunker, p. 20, pl. 1, fig. 5.
(?) 1839 *Pecten dextilis* Münster; Roemer, p. 28, pl. 28, figs. 24a–c.
1839 *Pecten vimineus* J. de C. Sowerby; Roemer, p. 29.
v*p 1850 *Pecten Palaemon* sp. nov; d'Orbigny, v. 1, p. 238 (Boule, 1908, v. 3, p. 37, pl. 18, fig. 5, non fig. 6).
v* 1850 *Pecten Phillis* sp. nov; d'Orbigny, v. 1, p. 257.
v 1850 *Pecten articulatus* (Schlotheim); d'Orbigny, v. 1, p. 285 (non Schlotheim sp.).
v* 1850 *Pecten Luciensis* sp. nov; d'Orbigny, v. 1, p. 314 (Boule, 1912, v. 7, p. 91, pl. 2, fig. 28).
v* 1850 *Pecten Camillus* sp. nov; d'Orbigny, v. 1, p. 342 (Boule, 1925, v. 14, p. 160, pl. 20, figs. 7–10).
v 1850 *Pecten vimineus* J. de C. Sowerby; d'Orbigny, v. 1, p. 373.
v* 1850 *Pecten Opis* sp. nov; d'Orbigny, v. 1, p. 374 (Boule, 1928, v. 17, p. 49, pl. 6, figs. 10, 11).
v* 1850 *Pecten subarticulatus* sp. nov; d'Orbigny, v. 2, p. 22 (Boule, 1929, v. 18, p. 171, pl. 19, figs. 13, 14).
v* 1850 *Pecten Nisus* sp. nov; d'Orbigny, v. 2, p. 22 (Boule, 1929, v. 18, p. 172, pl. 20, fig. 2).
1850 *Pecten Nothus* sp. nov; d'Orbigny, v. 2, p. 22 (Boule, 1929, v. 18, p. 173, pl. 20, fig. 3).
v* 1850 *Pecten Niso* sp. nov; d'Orbigny, v. 2, p. 22 (Boule, 1929, v. 18, p. 173, pl. 20, fig. 4).
1851 *Pecten ambiguus* Münster; Schafhautl, p. 410.
1852 *Pecten textorius* (Schlotheim); Verneuil and Collomb, p. 112.
1853 *Pecten textorius* (Schlotheim); Chapuis and Dewalque, p. 209, pl. 23, fig. 2.
1853 *Pecten articulatus* (Schlotheim); Chapuis and Dewalque, p. 212, pl. 29, fig. 3 (non Schlotheim sp.).
1853 *Pecten articulatus* (Schlotheim); Morris and Lycett, p. 32, pl. 33, fig. 12 (non Schlotheim sp.).
v* 1855 *Pecten icaunensis* sp. nov; Cotteau, p. 110.

v 1855 *Pecten desmoulinsianus* sp. nov; Cotteau, p. 112.
1855 *Pecten texturatus* Münster; Terquem, p. 322.
? 1855 *Pecten dispar* sp. nov; Terquem, p. 323, pl. 23, fig. 6
? 1858 *Pecten Trigeri* sp. nov; Oppel, p. 103.
1858 *Pecten Dewalquei* sp. nov; Oppel, p. 420.
pv 1858 *Pecten textorius* (Schlotheim); Quenstedt, p. 78, pl. 9, fig. 12, p. 500, pl. 67, fig. 5, p. 794, pl. 98, fig. 3.
1858 *Pecten textorius* γ var. nov; Quenstedt, p. 147, pl. 18, fig. 17.
1858 *Pecten textorius torulosi* subsp. nov; Quenstedt, p. 311, pl. 42, fig. 10.
v* 1858 *Pecten textorius albus* subsp. nov; Quenstedt, p. 627, pl. 77, figs. 25, 26.
v 1858 *Pecten dentatus* J. de C. Sowerby; Quenstedt, p. 753, pl. 92, fig. 3 (non J. de C. Sowerby sp.).
v 1858 *Pecten articulatus* (Schlotheim); Quenstedt, p. 754, pl. 92, fig. 11 (non Schlotheim sp.).
1858 *Pecten subtextorius* Münster; Quenstedt, p. 754, pl. 92, fig. 4.
v* 1858 *Pecten subtextorius Schnaitheimensis* subsp. nov; Quenstedt, p. 754, pl. 92, fig. 7.
1859 *Pecten Benedicti* sp. nov; Contejean, p. 313, pl. 23, figs. 13–15.
1859 *Pecten Billoti* sp. nov; Contejean, p. 315, pl. 23, figs. 22–24.
1860 *Pecten virguliferus* Phillips; Coquand, p. 68.
1860 *Pecten vimineus* J. de C. Sowerby; Coquand, p. 73.
1860 *Pecten subarticulatus* d'Orbigny; Coquand, p. 79.
1860 *Pecten Nisus* d'Orbigny; Coquand, p. 79.
1860 *Pecten Niso* d'Orbigny; Coquand, p. 79.
1860 *Pecten Billoti* Contejean; Coquand, p. 91.
1861 *Pecten subtextorius* Münster; Trautschold, p. 446.
1861 *Pecten subreticulatus* sp. nov; Stoliczka, p. 196, pl. 6, figs. 1, 2.
1861 *Pecten Rollei* sp. nov; Stoliczka, p. 197, pl. 6, figs. 5, 6.
1861 *Pecten verticillus* sp. nov; Stoliczka, p. 197, pl. 6, figs. 3, 4.
1861 *Pecten palosus* sp. nov; Stoliczka, p. 197, pl. 6, fig. 8.
1862 *Pecten articulatus* (Schlotheim); Thurmann and Étallon, p. 255, pl. 36, fig. 2 (non Schlotheim sp.).
1862 *Pecten Schnaitheimensis* Quenstedt; Thurmann and Étallon, p. 255, pl. 36, fig. 3.
1862 *Pecten subtextorius* Münster; Thurmann and Étallon, p. 256, pl. 36, fig. 4.
1862 *Pecten vimineus* J. de C. Sowerby; Thurmann and Étallon, p. 256, pl. 36, fig. 5.
1862 *Pecten Hermanciae* sp. nov; Étallon in Thurmann and Étallon, p. 256, pl. 36, fig. 6.
1863 *Pecten textorius* (Schlotheim); Schlönbach, p. 543.
1863 *Pecten splendens* sp. nov; Dollfus, p. 78, pl. 14, figs. 7–9.
1864 *Pecten securis* sp. nov; Dumortier, p. 68, pl. 8, figs. 9–11.
1864 *Pecten vimineus* J. de C. Sowerby; v. Seebach, p. 97.
1865 *Pecten canaliculatus* sp. nov; Terquem and Piette, p. 102, pl. 11, figs. 30–32.
(?) 1865 *Pecten dispar* Terquem; Terquem and Piette, p. 103.
1866 *Pecten Sismondae* sp. nov; Capellini, p. 481, pl. 6, figs. 4–6.
1867 *Pecten textorius* (Schlotheim); Dumortier, pp. 71, 125, pl. 13, fig. 1.
1868 *Pecten textorius* (Schlotheim); Jaubert, p. 235.
1869 *Pecten textorius* (Schlotheim); Dumortier, p. 139, pl. 22, fig. 2, p. 303, pl. 39, figs. 1, 2.
1869 *Pecten Rollei* Stoliczka; Dumortier, p. 139, pl. 22, fig. 1.
1869 *Pecten Fortunatus* sp. nov; Dumortier, p. 140, pl. 22, fig. 4.
1869 *Pecten semispinatus* sp. nov; Terquem and Jourdy, p. 130, pl. 13, figs. 21, 22.
1872 *Pecten Nisus* d'Orbigny; de Loriol et al., p. 385, pl. 22, fig. 14.
1874 *Pecten Ponzii* sp. nov; Gemmellaro, p. 107, pl. 13, fig. 5.
1874 *Pecten anastomoplicus* sp. nov; Gemmellaro and Di Blasi, p. 99, pl. 1, figs. 4–7.
1874 *Pecten erctensis* sp. nov; Gemmellaro and Di Blasi, p. 102, pl. 1, figs. 8–10.
1874 *Pecten textorius* (Schlotheim); Dumortier, pp. 193, 310, pl. 44, fig. 12.
1875 *Pecten vimineus* J. de C. Sowerby; de Loriol and Pellat, p. 204, pl. 23, figs. 3–5.
v* 1875 *Pecten Quenstedti* sp. nov; Blake, p. 231.
1878 *Pecten (Chlamys) Veneris* sp. nov; Gemmellaro and Di Blasi in Gemmellaro, p. 396, pl. 30, figs. 11, 12.
1878 *Pecten subtextorius* Münster; de Loriol, p. 161, pl. 23, figs. 1, 2.
? 1878 *Pecten Janiformis* sp. nov; Lundgren, p. 39, pl. 1, figs. 58, 59.
1879 *Pecten* cf. *textorius* (Schlotheim); Neumayr, p. 14.
1879 *Pecten Lotharingicus* sp. nov; Branco, p. 111, pl. 8, fig. 9.
1881 *Pecten subreticulatus* Stoliczka; J. Meneghini, p. 162, pl. 28, figs. 13, 14.
1881a *Pecten* aff. *vimineus* J. de C. Sowerby; Boehm, p. 183, pl. 40, figs. 3a, 3b.
v* 1881a *Pecten paraphoros* sp. nov; Boehm, p. 183, pl. 40, fig. 7.
1883 *Pecten* cf. *vimineus* J. de C. Sowerby; Lahusen, p. 23, pl. 1, fig. 17.
1883 *Pecten* n. sp.; Boehm, p. 614, pl. 67, figs. 36–38.
v 1883 *Pecten* aff. *vimineus* J. de C. Sowerby; Boehm, p. 615, pl. 68, figs. 1–4.
1883 *Pecten* cf. *vimineus* J. de C. Sowerby; Lahusen, p. 23, pl. 1, fig. 17.
1886 *Pecten* cf. *textorius* (Schlotheim); Sacco, p. 25.
v* 1886 *Pecten lacunarius* sp. nov; Rothpletz, p. 169, pl. 14, figs. 18, 18a, 20.
v 1888 *Pecten ambiguus* Münster; Schlippe, p. 129, pl. 2, fig. 9.
1888 *Pecten Dewalquei* Oppel; Schlippe, p. 130, pl. 2, fig. 10.
1892 *Pecten (Chlamys) Rollei* Stoliczka; Parona, p. 14, pl. 1, fig. 3.
1893 *Chlamys (Pecten) subtextoria* (Münster); Siemiradzki, p. 118.
1893 *Pecten Dewalquei* var. *Jurensis* var. nov; Riche, p. 97, pl. 1, figs. 17, 18.
v* 1893 *Pecten pelops* sp. nov; de Loriol in de Loriol and Lambert, p. 144, pl. 10, fig. 7.
1893 *Pecten subarticulatus* d'Orbigny; de Loriol, p. 303, pl. 32, figs. 16, 17.
1893 *Pecten Ferax* sp. nov; de Loriol, p. 308, pl. 33, fig. 1.
1894 *Pecten textorius* (Schlotheim); Möricke, p. 37.
v* 1894 *Pecten episcopalis* sp. nov; de Loriol, p. 50, pl. 6, figs. 1, 2.
1894 *Pecten* cfr. *nattheimensis* sp. nov; de Loriol, p. 52, pl. 6, figs. 4–6.

1894 *Pecten bipartitus* sp. nov; Futterer, p. 32, pl. 5, figs. 4, 4a.

1895 *Pecten Guyoti* sp. nov; de Loriol, p. 42, pl. 10, fig. 2.

1897 *Pecten textorius* (Schlotheim); Pompeckj, p. 773.

1898 *Pecten (Chlamys) silanus* sp. nov; Greco, p. 111, pl. 8, figs. 34, 35.

1898 *Pecten articulatus* (Schlotheim); Greppin, p. 128 (non Schlotheim sp.).

non 1903 *Pecten (Chlamys) dispar* Terquem; Bistram, p. 36, pl. 3, fig. 3.

1903 *Pecten textorius* (Schlotheim); Burckhardt, p. 7.

1903 *Pecten moravicus* sp. nov; Remes, p. 203, pl. 19, figs. 9a, 9b.

1903 *Pecten strambergensis* sp. nov; Remes, p. 204, pl. 19, figs. 10a–c.

v* 1904 *Pecten (Chlamys) Etiveyensis* sp. nov; de Loriol, p. 221, pl. 24, fig. 1.

1904 *Pecten (Chlamys) episcopalis* de Loriol; de Loriol, p. 223, pl. 24, fig. 7.

1904 *Pecten (Chlamys) blyensis* sp. nov; de Loriol, p. 224, pl. 24, fig. 3.

1904 *Pecten (Chlamys) Bourgeati* sp. nov; de Loriol, p. 225, pl. 24, figs. 5, 6.

(?) 1904 *Chlamys* cf. *dispar* (Terquem); Cossmann, p. 504.

1905 *Pecten (Chlamys) Dewalquei* Oppel; Kilian and Guébhard, p. 743.

1905 *Pecten (Chlamys)* voisin de *Nattheimensis* de Loriol; Kilian and Guébhard, p. 817.

1905 *Pecten (Chlamys) vimineus* J. de C. Sowerby; Kilian and Guébhard, p. 817.

v 1905 *Pecten subarticulatus* d'Orbigny; Peron, p. 217, pl. 10, fig. 2.

v 1905 *Pecten vimineus* J. de C. Sowerby; Peron, p. 222.

v 1905 *Pecten etiveyensis* de Loriol; Peron, p. 227, pl. 10, figs. 3, 4.

v 1905 *Pecten desmoulinsianus* Cotteau; Peron, p. 233, pl. 5, fig. 15, pl. 10, fig. 7.

1906 *Pecten Ugolinii* sp. nov; Fucini, p. 620, pl. 11, fig. 4.

? 1906 *Pecten capillatus* sp. nov; Fucini, p. 622, pl. 11, fig. 5.

(?) 1907 *Pecten (Chlamys) dispar* Terquem; Joly, p. 75.

1907 *Chlamys textoria* (Schlotheim); Riaz, p. 620.

1907b *Chlamys subarticulata* (d'Orbigny); Cossmann, p. 1, pl. 2, figs. 1, 2.

1907b *Chlamys camillus* (d'Orbigny); Cossmann, p. 2, pl. 2, fig. 7.

1907b *Chlamys* cf. *stricta* (Münster); Cossmann, p. 2, pl. 2, fig. 5 (non Münster sp.).

1910 *Chlamys dewalquei* (Oppel); Lissajous, p. 360, pl. 10, fig. 3.

1910 *Chlamys subtextoria* (Münster); Lissajous, p. 360, pl. 10, fig. 4.

1911 *Pecten (Chlamys) protextorius* sp. nov; Rollier, p. 264.

1911 *Pecten (Chlamys) jurensis* Riche;Rollier, 265.

1911 *Pecten (Chlamys) Schombergensis* sp. nov; Rollier, p. 266.

1911 *Pecten (Chlamys) Brisgoviensis* sp. nov; Rollier, p. 267.

1911 *Pecten (Chlamys) Schlippei* sp. nov; Rollier, p. 267.

1911 *Pecten (Chlamys) Lycetti* sp. nov; Rollier, p. 267.

1911 *Chlamys bathonica* sp. nov; Cossmann, p. 1, pl. 1, figs. 1–4.

1914 *Chlamys Gadoisi* sp. nov; Cossmann, p. 3, pl. 5, fig. 2.

non 1915 *Pecten vimineus* J. de C. Sowerby; Krenkel, p. 300, pl. 25, fig. 41.

1915 *Pecten (Chlamys)* sp. indet; Rollier, pl. 31, fig. 2.

non 1916 *Chlamys (Pseudamussium) palaemon* (d'Orbigny); Cossmann, p. 46, pl. 5, figs. 18–20.

1916 *Pecten textorius* (Schlotheim); Jaworski, p. 436.

1916 *Pecten textorius* var. *torulosa* Quenstedt; Jaworski, p. 437.

1916 *Chlamys articulata* (Schlotheim); Paris and Richardson, p. 524.

v* 1916 *Chlamys articulata* var. *notgroviensis* var. nov; Paris and Richardson, p. 525, pl. 45, fig. 2.

v* 1916 *Chlamys articulata* var. *sauzeana* var. nov; Paris and Richardson, p. 526, pl. 45, figs. 3a, 3b.

1916 *Chlamys ambigua* (Münster); Paris and Richardson, p. 526.

v* 1916 *Eopecten articulatus* sp. nov; Paris and Richardson, p. 531, pl. 44, fig. 5.

1917 *Pecten peruanus* sp. nov; Tilmann, p. 673, pl. 24, figs. 4a, 4b, 5.

1917 *Pecten Lahuseni* sp. nov; Borissiak and Ivanoff, p. 11, pl. 2, figs. 9, 9a.

1917 *Pecten pseudotextorius* Redlich; Borissiak and Ivanoff, p. 15, pl. 2, fig. 12.

1917 *Pecten ambiguus* Münster; Borissiak and Ivanoff, p. 16, pl. 2, fig. 8.

1917 *Pecten subambiguus* sp. nov; Borissiak and Ivanoff, p. 18, pl. 2, figs. 7, 7a.

1920 *Pecten anastomoplicus* Gemmellaro and Di Blasi; Faure-Marguerit, p. 54.

1920 *Pecten strambergensis* Remes; Faure-Marguerit, p. 57.

1920 *Pecten moravicus* Remes; Faure-Marguerit, p. 58.

1920 *Pecten vimineus* J. de C. Sowerby; Faure-Marguerit, p. 58.

1920 *Pecten* aff. *vimineus* J. de C. Sowerby; Faure-Marguerit, p. 59.

1920 *Pecten articulatus* (Schlotheim); Faure-Marguerit, p. 59.

1920 *Pecten articulatus* var. passsant à *P. anastomoplicus* Gemmellaro; Faure-Marguerit, p. 59.

1920 *Pecten (Chlamys) subtextorius* Münster; Faure-Marguerit, p. 60.

1920 *Pecten Rolleiformis* sp. nov; Fucini, p. 90, pl. 5, figs. 15, 16.

1923 *Pecten (Chlamys) torulosi* Quenstedt; Ernst, p. 52, pl. 1, fig. 8.

1923 *Chlamys Dewalquei* (Oppel); Lissajous, p. 158, pl. 30, figs. 3, 3a.

1926 *Chlamys textoria* (Schlotheim); Staesche, p. 30.

v 1926 *Chlamys* aff. *textoriae* (Schlotheim); Staesche, p. 30, pl. 1, figs. 8, 9.

v 1926 *Chlamys torulosi* (Quenstedt); Staesche, p. 33, pl. 1, fig. 1.

1926 *Chlamys* cf. *Phillis* (d'Orbigny); Staesche, p. 34, pl. 1, fig. 12.

1926 *Chlamys Dewalquei* (Oppel); Staesche, p. 35.

v 1926 *Chlamys ambigua* (Münster); Staesche, p. 36, pl. 1, fig. 2.

v 1926 *Chlamys Rosimon* (d'Orbigny); Staesche, p. 38, pl. 2, fig. 1 (non d'Orbigny sp.).

v 1926 *Chlamys* aff. *Lotharingicae* (Branco); Staesche, p. 38, pl. 1, figs. 5, 6.

1926 *Chlamys Meriani* (Greppin); Staesche, p. 39, pl. 1, fig. 3 (non Greppin sp.).

1926 *Chlamys subtextoria* (Münster); Staesche, p. 40.

1926 *Chlamys paraphora* (Boehm); Staesche, p. 41.

1926 *Chlamys Schnaitheimensis* (Quenstedt); Staesche, p. 42.

pv 1926 *Chlamys Nattheimensis* (de Loriol); Staesche, p. 42, pl. 1, fig. 13, pl. 2, fig. 2.

v 1926 *Chlamys Quenstedti* (BLAKE); STAESCHE, p. 44, pl. 1, fig. 7.
1926 *Chlamys* cf. *episcopalis* (DE LORIOL); STAESCHE, p. 45, pl. 2, fig. 3.
? 1926 *Chlamys Trigeri* (OPPEL); STAESCHE, p. 56.
1926 *Chlamys textoria* (SCHLOTHEIM); ROMAN, pp. 113, 140, 168.
1926 *Chlamys ambigua* (MÜNSTER); ROMAN, p. 155.
1926 *Chlamys subtextoria* (MÜNSTER); ROMAN, pp. 193, 196, 197.
1926 *Pecten vimineus* J. DE C. SOWERBY; ROMAN, p. 197.
1928 *Chlamys* cf. *vimineus* (J. DE C. SOWERBY); DOUGLAS and ARKELL, p. 136.
1929 *Pecten (Chlamys) textorius* (SCHLOTHEIM); LANQUINE, pp. 82, 84, 188.
1929 *Pecten (Chlamys) Dewalquei* OPPEL; LANQUINE, pp. 131, 199, 300, 310, 324.
1929 *Pecten (Chlamys) ambiguus* (MÜNSTER); LANQUINE, pp. 300, 324.
1929 *Pecten (Chlamys)* cf. *Jurensis* RICHE; LANQUINE, p. 300.
1930a *Chlamys (Chlamys) nattheimensis* (DE LORIOL); ARKELL, p. 104, pl. 10, figs. 6–8.
v 1931a *Chlamys (Chlamys) splendens* (DOLLFUS); ARKELL, p. 107, pl. 10, figs. 1–5, pl. 14, fig. 5.
v 1931a *Chlamys (Chlamys)* cf. *blyensis* (DE LORIOL); ARKELL, p. 110, pl. 11, figs. 1, 1a.
1931 *Pecten vimineus* J. DE C. SOWERBY; YIN, p. 121.
1931 *Pecten strambergensis* REMES; YIN, p. 122, pl. 12, fig. 8.
1932 *Pecten (Chlamys) textoria* (SCHLOTHEIM); TZANKOV and BONCEV, p. 230, pl. 1, fig. 8.
1933 *Pecten (Chlamys)* sp. – *subtextoria* group; DIETRICH, p. 64, pl. 9, fig. 35.
1934 *Chlamys* cf. *textoria* (SCHLOTHEIM); ROSENKRANTZ, p. 113.
1934 *Chlamys rollei* (STOLICZKA); ROSENKRANTZ, p. 113.
1935a *Chlamys* cf. *splendens* (DOLLFUS); COX, p. 175, pl. 18, fig. 10.
1935b *Chlamys* sp.; COX, p. 13, pl. 2, fig. 7.
1936 *Aequipecten* sp; WANDEL, p. 483, pl. 15, fig. 3.
v 1936 *Chlamys textorius* (SCHLOTHEIM); DECHASEAUX, p. 13, pl. 1, figs. 1–4.
v 1936 *Chlamys ambiguus* (MÜNSTER); DECHASEAUX, p. 14, pl. 2, fig. 2, pl. 3, fig. 1.
v 1936 *Chlamys Dewalquei* (OPPEL); DECHASEAUX, p. 15, pl. 1, figs. 5, 7, pl. 2, fig. 4.
1936 *Chlamys lotharingicus* (BRANCO); DECHASEAUX, p. 17.
1936 *Chlamys Camillus* (D'ORBIGNY); DECHASEAUX, p. 18.
1936 *Chlamys episcopalis* (DE LORIOL); DECHASEAUX, p. 18.
v 1936 *Chlamys etiveyensis* (DE LORIOL); DECHASEAUX, p. 18, pl. 3, figs. 3, 4.
1936 *Chlamys subtextorius* (MÜNSTER); DECHASEAUX, p. 19, pl. 3, fig. 2.
1936 *Chlamys splendens* (DOLLFUS); DECHASEAUX, p. 20.
v 1936 *Chlamys Blyensis* (DE LORIOL); DECHASEAUX, p. 20, pl. 3, fig. 8.
v 1936 *Chlamys subarticulatus* (D'ORBIGNY); DECHASEAUX, p. 21, pl. 3 figs. 5, 6.
v 1936 *Chlamys Nattheimensis* (DE LORIOL); DECHASEAUX, p. 22, pl. 3, fig. 7.
. 1936 *Chlamys Nisus* (D'ORBIGNY); DECHASEAUX, p. 23.
1936 *Chlamys Guyoti* (DE LORIOL); DECHASEAUX, p. 24.
v 1936 *Chlamys Bourgeati* (DE LORIOL); DECHASEAUX, p. 24, pl. 3, fig. 10.
1936 *Chlamys* sp; DECHASEAUX, p. 24, pl. 4, fig. 1.
(?) 1936 *Pecten (Chlamys) dispar* TERQUEM; DECHASEAUX, p. 27.
v* 1936 *Chlamys neumarktensis* sp. nov; KÜHN, p. 247, pl. 12, fig. 40.
1938 *Chlamys Dewalquei* (OPPEL); CHOUBERT, p. 198.
1938 *Chlamys* cf. *ambigua* (MÜNSTER); WEIR, p. 47, pl. 3, figs. 9, 10.
1942 *Pecten (Chlamys) textorius* (SCHLOTHEIM); LEANZA, p. 172, pl. 7, fig. 2.
1942 *Pecten (Chlamys) textorius* var. *torulosa* QUENSTEDT; LEANZA, p. 173, pl. 7, fig. 4.
1948 *Chlamys viminea* (J. DE C. SOWERBY); COX and ARKELL, p. 11.
1948 *Chlamys ambigua* (MÜNSTER); COX and ARKELL, p. 12.
1948 *Chlamys jurensis* (RICHE); COX and ARKELL, p. 12.
1948 *Chlamys subtextoria* (MÜNSTER); COX and ARKELL, p. 12.
1951 *Chlamys torulosi* (QUENSTEDT); MAUBERGE, p. 367.
1951 *Chlamys textoria* (SCHLOTHEIM); TROEDSSON, p. 213, pl. 21, figs. 14–16.
1952 *Chlamys ambigua* (MÜNSTER); COX, p. 4, pl. 1, figs. 2–4.
1952 *Chlamys subtextoria* (MÜNSTER); COX, p. 6, pl. 1, figs. 5–7.
1952 *Chlamys* cf. *episcopalis* (DE LORIOL); COX, p. 7, pl. 1, fig. 1.
1952 *Chlamys* sp. indet; COX, p. 9, pl. 1, fig. 8.
? 1953 *Chlamys (Chlamys) wunschae* sp. nov; MARWICK, p. 98, pl. 10, figs. 23, 24.
1956 *Chlamys subulata securis* (DUMORTIER); MELVILLE, p. 121, pl. 5, figs. 4, 5.
1957 *Chlamys kurumensis* sp. nov; KOBAYASHI and HAYAMI in HAYAMI, p. 119, pl. 20, figs. 1a, 1b.
1961 *Chlamys textoria* (SCHLOTHEIM); HAYAMI, pp. 254, 318, 319.
1961 *Chlamys dewalquei* var. *jurensis* (RICHE); BARBULESCU, p. 702.
1964 *Chlamys luciensis* (D'ORBIGNY); J.-C. FISCHER, p. 17, pl. 1, figs. 14, 15.
1965 *Chlamys subtextoria* (MÜNSTER); COX, p. 55, pl. 7, fig. 8.
1966 *Chlamys textorius* (SCHLOTHEIM); BEHMEL and GEYER, p. 28.
1966 *Chlamys torulosi* (QUENSTEDT); BEHMEL and GEYER, p. 28.
1967 *Chlamys textoria* (SCHLOTHEIM); BERRIDGE and IVIMEY-COOK, p. 160.
1968 *Chlamys textoria* (SCHLOTHEIM); WOBBER, p. 36.
1970 *Chlamys* cf. *nattheimensis* (DE LORIOL); BEHMEL, p. 62.
1970 *Chlamys* cf. *quenstedti* (BLAKE); BEHMEL, p. 62.
1971 *Chlamys* cf. *textoria* (SCHLOTHEIM); HALLAM, pp. 242–244, 246, 247.
1973 *Entolium* (?) *Stoliczkai* (GEMMELLARO); LENTINI, p. 27, pl. 16, fig. 1 (non GEMMELLARO sp.).
1973 *Chlamys (Aequipecten)* cfr. *Pollux* (D'ORBIGNY); LENTINI, p. 27, pl. 16, fig. 1 (non D'ORBIGNY sp.).
1973 *Chlamys (Velata)* cfr. *velata* (GOLDFUSS); LENTINI, p. 29, pl. 15, fig. 8 (non GOLDFUSS sp.).
1974 *Chlamys enantyi* sp. nov; SKWARKO, p. 83, pl. 26, figs. 1, 6, 12.
v 1975 *Chlamys subtextoria* (MÜNSTER); YAMANI, p. 56, pl. 2, figs. 15, 16.
v 1975 *Chlamys paraphora* (BOEHM); YAMANI, p. 57, pl. 2, fig. 18.
v 1975 *Chlamys quenstedti* (BLAKE); YAMANI, p. 58, pl. 2, figs. 1, 2.

v*? 1978 *Chlamys (Chlamys) bedfordensis* sp. nov; Duff, p. 69, pl. 5, figs. 14–16, 18, 21, text fig. 23.

Lectotype of *Pectinites textorius* Schlotheim 1820, p. 229 designated herein; HM-M23; Pl. 8, Fig. 20 herein; H: 55, L: 51; L. Lias, Amberg (Franconia).

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

‚Aus älterem Flötzkalk (sogenannten Gryphitenkalk) von Amberg, theils der Gebirgsart aufliegend, theils in freyen Exemplaren, mit versteinerter Schale, jedoch etwas schädigt, und einige mit beyden Hälften (4 Ex.).

In der Form und Querstreifung dem *Pectin. asper* ähnlich, aber die Beschaffenheit und Richtung der Strahlen sehr verschieden. Sie sind ungleich dünner, liegen viel enger zusammen, und zwischen jedem etwas stärkeren und hervorspringenden wird abwechselnd ein etwas tiefer liegender, feinerer sichtbar. Äußerst feine, scharf hervortretende Querstreifen, welche eng zusammenlaufen, und auf jedem Längenstrahl kleine hervorstehende Schuppen bilden, geben dem Ganzen ein gestricktes oder gewebtes Ansehen. Beyde Hälften sind flach und gleichförmig gewölbt. Scheint nicht sehr häufig vorzukommen und ist in schön erhaltenen und vollständigen Exemplaren sehr selten.‘

2. AMENDED DIAGNOSIS

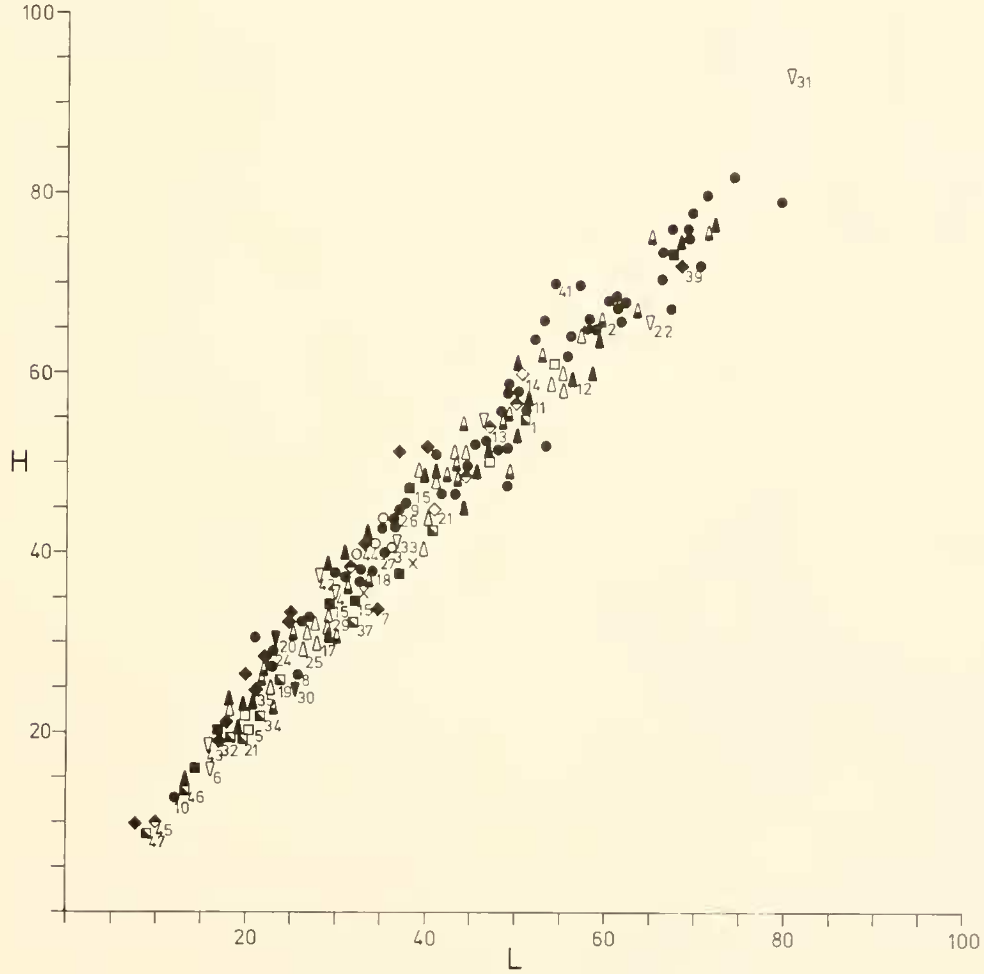
Distinguished from other Jurassic species of *Ch. (Chlamys)* by the presence of imbricate lamellae on the plicae.

3. AMENDED DESCRIPTION

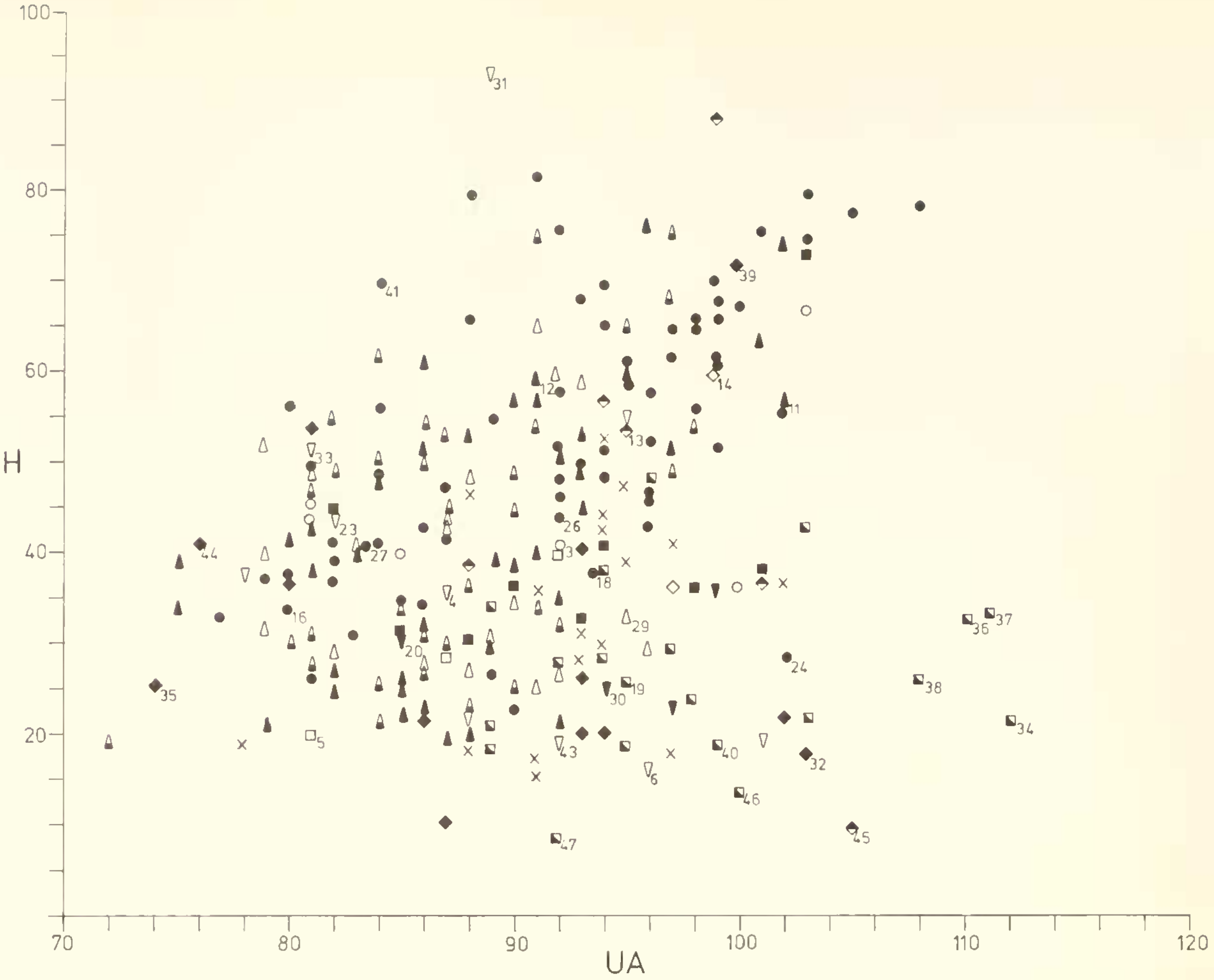
Disc shape variable, sub-orbicular early in ontogeny, becoming increasingly sub-ovate, higher than long (text fig. 148) towards the maximum height of 93.5 mm (GPIT 2-92-3). Umbonal angle increasing during ontogeny but very variable, tending to be relatively high in forms with many plicae (text figs. 149, 147). Dorsal margins concave; disc flanks low.

Approximately equilateral; inequivalve, left valve low-moderate convexity, right valve usually almost flat. Intersinal distance variable, greater in left valve than right, increasing isometrically in the former and at a decreasing rate with respect to length in the latter (text figs. 150, 151). Depth of byssal notch variable, moderate to large, but increasing with approximate isometry (text fig. 152).

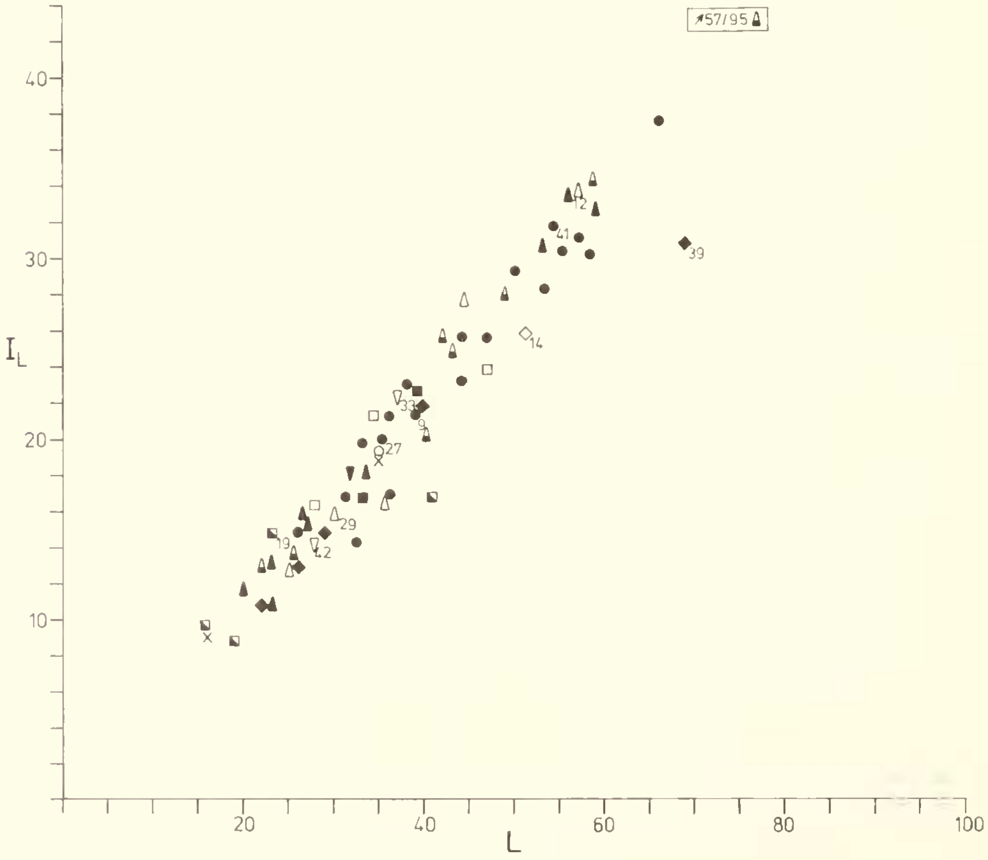
Auricles well demarcated from disc, variable in size. Both posterior auricles meeting hinge line at an obtuse angle and disc at an acute angle. Anterior auricles meeting disc at an acute angle and hingeline at a variable angle, 90° or less. All auricles bearing comarginal imbricate lamellae, anterior auri-



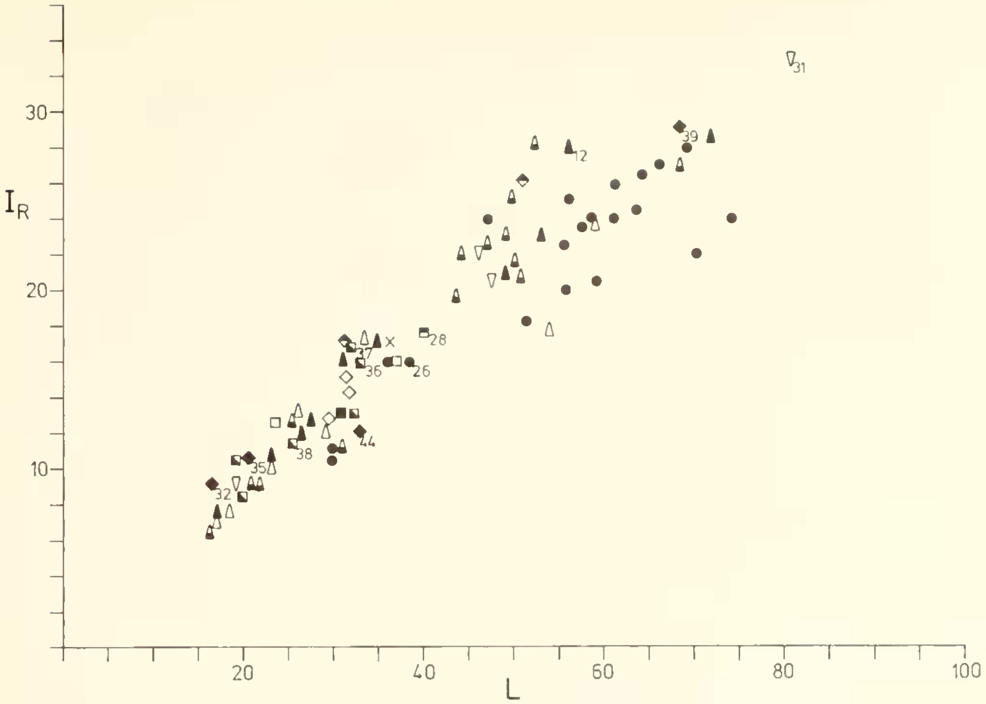
Text fig. 148: *Chlamys (Ch.) textoria* – height/length.



Text fig. 149: *Chlamys (Ch.) textoria* – height/umbonal angle.



Text fig. 150: *Chlamys (Ch.) textoria* – intersinal distance on left valve/length.



Text fig. 151: *Chlamys (Ch.) textoria* – intersinal distance on right valve/length.

cle of left valve also bearing radial striae of variable prominence. Anterior auricle height variable (text fig. 153). Anterior and posterior hinge lengths both variable, former increasing with respect to length at a slightly decreasing rate (text fig. 154), latter increasing at a slightly increasing rate (text fig. 155).

Disc exterior ornamented with a variable number of radial plicae, tending to increase in number by either intercalation or splitting but at a very variable rate (Pl. 6, Figs. 10–12, Pl. 7, Figs. 1–23, Pl. 8, Figs. 1–3, 5–20). Between 17 and 30 plicae at the earliest stages in ontogeny, between 17 and 98 at L: 20 (text fig. 146), between 17 and 121 at L: 40 (text fig. 146) and between 17 and at least 62 at L: 60 (text fig. 146). Plicae bearing variably spaced imbricate comarginal lamellae which tend to be closer and lower in forms with more plicae. Lamellae generally lower on right cf. left valves of all forms.

Shell thickness moderate.

4. DISCUSSION

The lectotype (herein designated) of *'Pectinites' textorius* Schlotheim (HM M23; Pl. 8, Fig. 20) is a poorly preserved specimen but the ornament and metric proportions (1) clearly fall within the range of the species described in Section 3. The latter, by reason of the historically senior position of Schlotheim's taxonomic species is therefore known hereinafter as *Chlamys (Ch.) textoria*.

The following type specimens cannot be separated from *Ch. (Ch.) textoria* by their metric proportions and their plical counts at the given length (in square brackets) also fall within the range of the species.

The sole known type of:

2. *'Pecten' vimineus* J. de C. Sowerby (BM 43318; Pl. 8, Figs. 1, 5) [21:60];

   the sole observed types of:
3. *'P.' ambiguus* Münster (BSPHG AS VII 620; Pl. 7, Fig. 17) [32: 36];
4. *'P.' subtextorius* Münster (BSPHG AS VII 623; Pl. 7, Fig. 16) [41: 30];

   the holotype (M) of:
5. *'P.' semispinatus* Terquem and Jourdy (ENSM L342; Pl. 7, Fig. 4) [22:20];

   the sole observed syntype of:
6. *'P.' paraphoros* Boehm (BSPHG) [43:16];

   the sole observed type of:
7. *'P.' pelops* de Loriol (MNS B.03982; Pl. 7, Fig. 6) [20:34];

   a possible syntype of:
8. *'P.' episcopalis* de Loriol (MNO 3761; Pl. 7, Fig. 18) [38:26];

   syntypes of:
9. *'P.' (Chlamys) Etiveyensis* de Loriol (MNS B.03986; Pl. 7, Fig. 22) [40:38];
10. *'P.' desmoulinsianus* Cotteau (MNS B.03987; Pl. 7, Figs. 2, 3) [18:12];

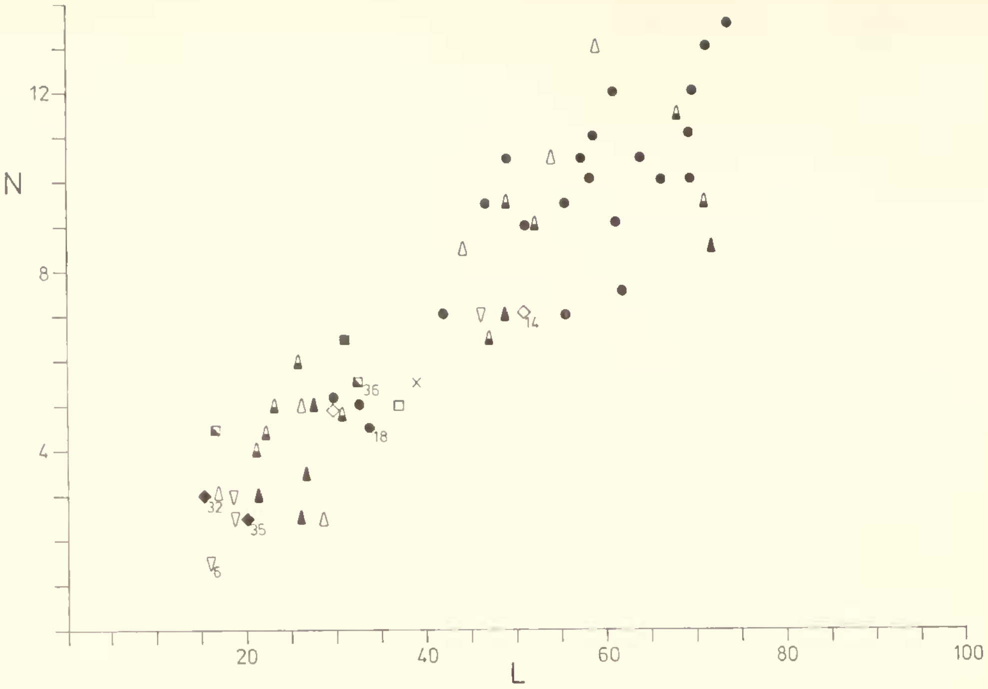
    the sole observed syntype of:
11. *Ch. articulata* var. *notgroviensis* Paris and Richardson (BM L41976; Pl. 7, Fig. 19) [27:51];

    the sole observed type of:
12. *Ch. articulata* var. *sauzeana* Paris and Richardson (BM L41978; Pl. 7, Figs. 1, 7) [21:56];

    the holotype (M) of:
13. *Ch. neumarktensis* Kuhn (BSPHG AS I 867; Pl. 7, Fig. 13) [26:48];

    the alleged holotype (M) of:
14. *'P.' texturatus* Münster (BSPHG AS VII 619; Pl. 7, Fig. 21) [46:63];

    and the syntypes of:



Text fig. 152: *Chlamys (Ch.) textoria* – depth of byssal notch/length.

15. *'P.' Phillis* d'Orbigny (MNO 2075A–C; Pl. 6, Fig. 10, Pl. 7, Fig. 5) [respectively 17:31, 19:39, 21:29].
16. *'P.' subarticulatus* d'Orbigny (MNO 4286, 4286A) [respectively 19:39, 19:30].

The original figures of the following are similarly inseparable:

17. *'P.' virguliferus* Phillips [39:20].
18. *'P.' subimbricatus* Roemer [60:33.5].
19. *'P.' palosus* Stoliczka [45:23].
20. *'P.' Sismondae* Capellini [36:23].
21. *'P.' Fortunatus* Dumortier [36:45].
22. *'P.' anastomoplicus* Gemmellaro and Di Blasi [20:65].
23. *'P.' erctensis* Gemmellaro and Di Blasi [32:37].
24. *'P.' Ferax* de Loriol [50:27].
25. *'P.' (Ch.) silanus* Greco [35:26].
26. *'P.' (Ch.) blyensis* de Loriol [36:38.5].
27. *'P.' (Ch.) Bourgeati* de Loriol [18:35].
28. *'P.' subambiguus* Borissiak and Ivanoff [19:40].

Metric proportions of the original figures of the following are inseparable from *Ch. (Ch.) textoria* but the number of plicae cannot be counted due to poor drawing, although it appears to be within the range of the latter species.

29. *'P.' textorius torulosi* Quenstedt.
30. *'P.' securis* Dumortier.

The following type specimens plot outside the range of text figs. 148–155 for the parameters stated but may be considered to be extreme variants of *Ch. (Ch.) textoria* since their plical counts at the lengths stated are within the ranges described in Section 3.

The holotype (M) of:

31. *'P.' Quenstedti* Blake GPIT 2-92-3; Pl. 6, Fig. 12), high H/UA [20:80.5];

the sole observed syntype of:

32. *'P.' textorius albus* Quenstedt (GPIT), low H/UA [47:16.5];

the sole observed type of:

33. *'P.' subtextorius Schnaitheimensis* Quenstedt (GPIT 4-92-7; Pl. 8, Fig. 13), high H/UA and HAA/L [43:27];

the sole observed syntype of:

34. *'P.' lacunarius* Rothpletz (BSPHG AS XXIV 52; Pl. 6, Fig. 11), low H/UA [25:22].

The following original figures are considered to be inseparable for the same reasons.

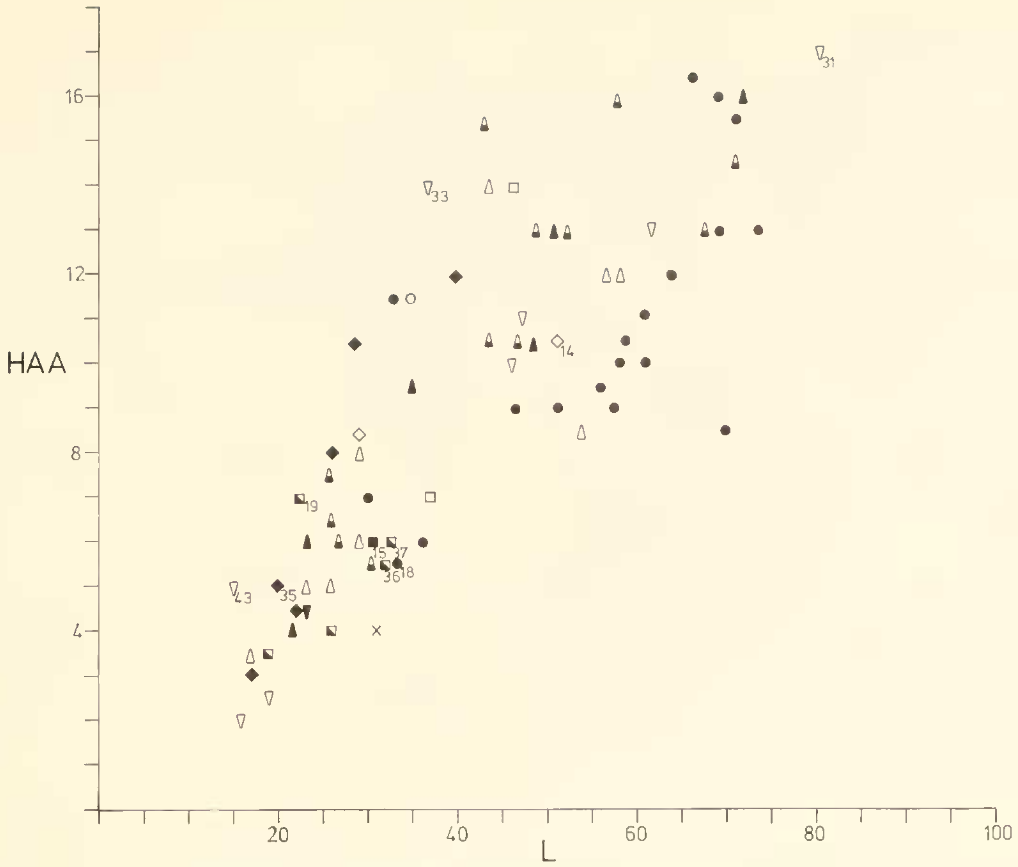
35. *'P.' Benedicti* Contejean, high H/UA [30:20.5].
36. *'P.' subreticulatus* Stoliczka, low H/UA [70:32.5].
37. *'P.' Rollei* Stoliczka, low H/UA [50:32].
38. *'P.' verticillus* Stoliczka, low H/UA [70:38].
39. *'P.' splendens* Dollfus, low I_L/L [30:68.5].
40. *'P.' (Ch.) Veneris* Gemmellaro and Di Blasi, low H/UA [80:19]).
41. *'P.' Guyoti* de Loriol, high H/L and H/UA [35:54].
42. *'P.' moravicus* Remes, high H/UA [25:28].
43. *'P.' strambergensis* Remes, high PH/L [18:15.5].

Although it has not been possible to accurately measure the number of plicae in the original figures of the following species, the overall density of the ornament (in square brackets) appears to be within the range of *Ch. (Ch.) textoria* and the anomalous metric proportions stated are probably a consequence of enlargement or distortion in illustration.

44. *'P.' Billoti* Contejean, high H/UA [coarse].
45. *'P.' Ponzii* Gemmellaro, low H/UA [fine].
46. *'P.' Ugolinii* Fucini, low H/UA [fine].

The figure of *'P.' capillatus* Fucini (47) also has low H/UA but the ornament is dense enough [40:9] to suggest that it may belong to a different species.

In cases 7, 14, 29, 30 and 40 above, the reduction or complete loss of the comarginal ornament is probably due to abrasion. In cases 13, 22, 23 and 31 the lack of comarginal orna-



Text fig. 153: *Chlamys (Ch.) textoria* – height of anterior auricle/length.

ment is due to preservation as internal moulds. In 18 and 43 the apparently larger size of the posterior compared to the anterior auricle is clearly due to reversal in printing and measurements have been correspondingly altered.

'*P.*' *vimineus* (2) has been used by Boehm (1881a) for forms said to have as few as 16 plicae (i. e. outside the range of *Ch. (Ch.) textoria*). Boehm's figures do not, however, support this claim since they depict specimens with 18–19 plicae. Krenkel (1915) has applied J. de C. Sowerby's specific name to forms which, by the irregularity of the ornament, are probably referable to *Eopecten*.

'*P.*' *Quenstedti* (31) was erected by Blake (1875) for the specimen which was incorrectly referred to '*P.*' *dentatus* J. de C. Sowerby by Quenstedt (1858). '*P.*' *moravicus* (42) was created by Remes (1903) for the original of '*P.*' n. sp. (Boehm, 1883), among other specimens.

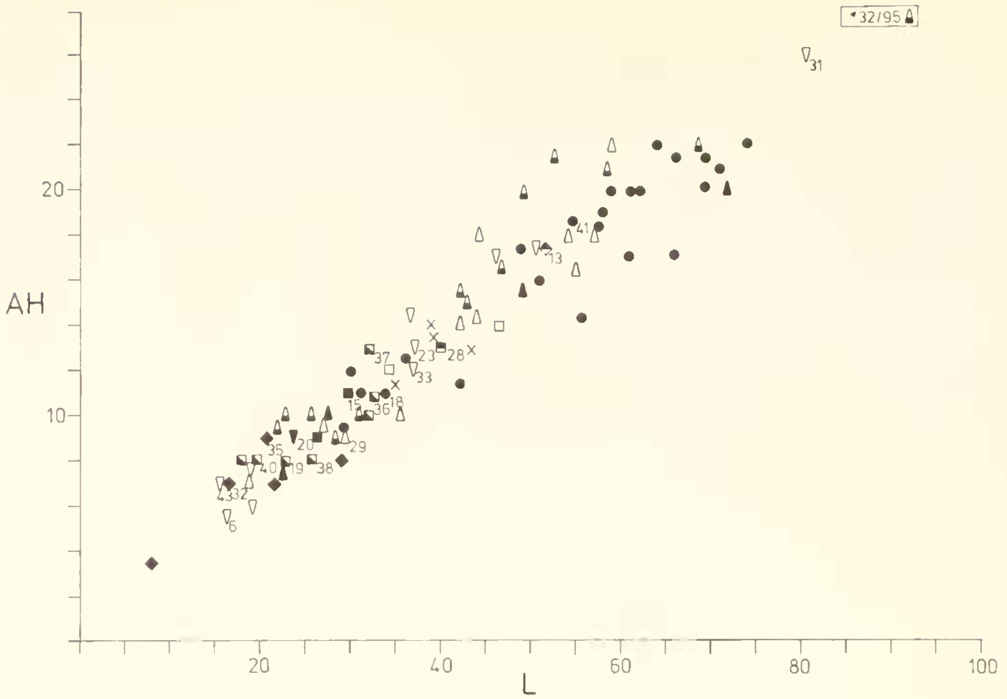
Quenstedt's subspecies '*P.*' *textorius torulosi* (29) and '*P.*' *subtextorius Schnaitheimensis* (33) were subsequently raised to specific rank by respectively Ernst (1923) and Thurmann and Étallon (1862). Although outside Quenstedt's hypodigm, Thurmann and Étallon's species (with 18 plicae throughout ontogeny) is within the present author's hypodigm for *Ch. (Ch.) textoria*. Varietal use of the name *torulosi* (see Synonymy) does not differ from the original hypodigm. Subspecific use of '*P.*' *securis* Dumortier (30) by Melville (1956) is also within the original hypodigm.

'*P.*' *(Ch.) Etiveyensis* de Loriol (9) was created for the holotype (M) of '*P.*' *icaunensis* Cotteau in the belief that the latter name was a junior homonym of a Neocomian species. In fact the Neocomian species was described after the Jurassic species in Cotteau's work (1855: 115) thus it could be argued that the latter is the *senior* homonym and that de Loriol's species is therefore a junior objective synonym which must be rejected.

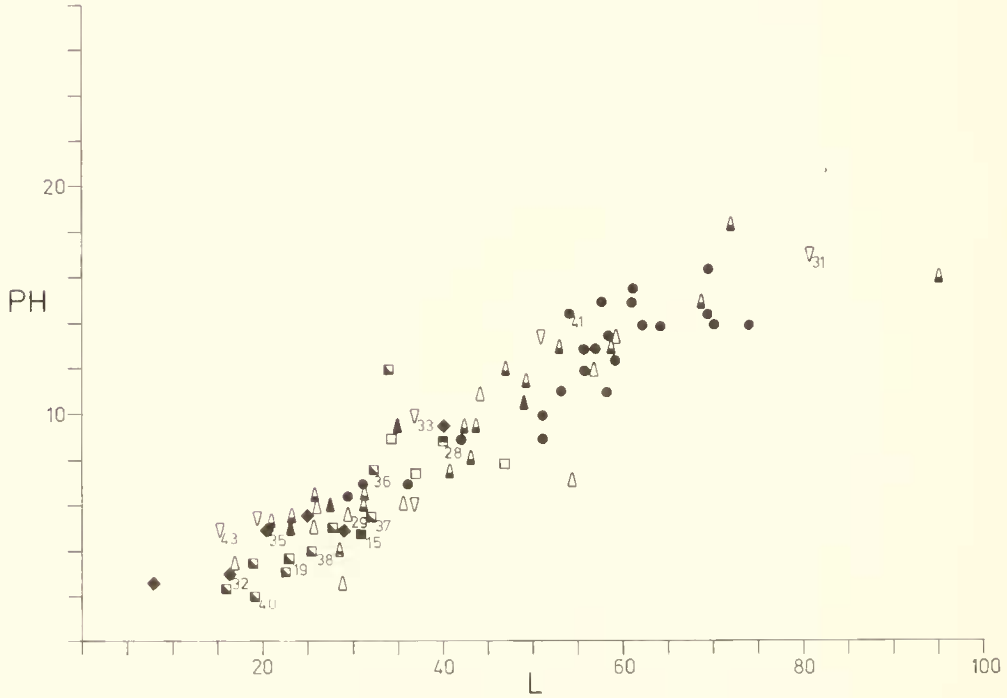
'*P.*' *subarticulatus* d'Orbigny (16) must be rejected since it is a junior primary homonym of a Valanginian species described by Roemer (1839).

The following specimens are too poorly preserved to allow measurement of the metric proportions plotted in text figs. 148–155. However the general form and number of plicae (in square brackets) is within the range of *Ch. (Ch.) textoria* of comparable size.

a. The syntypes of '*P.*' *Luciensis* d'Orbigny (MNO 2910) [20].
b. The syntypes pf '*P.*' *Camillus* d'Orbigny (MNO 3400A–D; Pl. 7, Fig. 10) [23–24].
c. The syntypes of '*P.*' *Opis* d'Orbigny (MNO 3762, 3762A, 3762B) [30].
d. The syntypes of '*P.*' *Nisus* d'Orbigny (MNO 4289) [19].
e. The syntypes of '*P.*' *Niso* d'Orbigny (MNO 4291, 4291A) [39].
f. The sole observed type of '*Eopecten*' *articulatus* Paris and Richardson (BM L42060; Pl. 8, Fig. 2) [21].
g. The original of *Ch. Rosimon* (d'Orbigny); Staesche (GPIT 1592/5; Pl. 8, Fig. 16) [48].
h. The original of *Ch.* sp., Dechaseaux [18].



Text fig. 154: *Chlamys (Ch.) textoria* – anterior hinge length/length.



Text fig. 155: *Chlamys (Ch.) textoria* – posterior hinge length/length.

The original figures of the following are poor illustrations or depict incompletely preserved specimens. However, they are similarly inseparable from *Ch. (Ch.) textoria*.

i. '*P.*' *varius* LINNAEUS; YOUNG and BIRD (non LINNAEUS) [23].
j. '*P.*' *elegans* YOUNG and BIRD [27].
k. '*P.*' *textorius* var. *orbicularis* KOCH and DUNKER [43].
l. '*P.*' *Nothus* D'ORBIGNY in BOULE [19].
m. '*P.*' *Hermanciae* ÉTALLON [25].
n. '*P.*' *Janiformis* LUNDGREN [20].
o. '*P.*' *Lotharingicus* BRANCO [22].
p. '*P.*' *bipartitus* FUTTERER [28].
q. *Ch.* cf. *stricta* (MÜNSTER); COSSMANN (non MÜNSTER) [35].
r. *Ch. Gadoisi* COSSMANN [22].
s. '*P.*' *(Ch.)* sp. indet; ROLLIER [22].
t. '*P.*' *Lahuseni* BORISSIAK and IVANOFF [27].
u. '*P.*' *Rolleiformis* FUCINI [30].
v. *Ch.* sp; COX [27].
w. '*Aequipecten*' sp; WANDEL [20].
x. *Ch.* sp; DECHASEAUX [18].
y. *Ch.* sp. indet; COX [19].
z. *Ch. kurumensis* KOBAYASHI and HAYAMI [42].
a_1. *Ch. enantyi* SKWARKO [30].

The reduced development of comarginal ornament in a, l, o, u and x can be attributed to abrasion. However, the smoothness of the right valve compared to the strong ornamentation of the left in *'P.' Janiformis* (n) may be indicative of a specific difference. The irregular plication of *E. articulatus* (f) is only known in two specimens and may be caused by restricted growth amongst corals (see Section 8).

One of the original syntypes of *'P.' Nothus* (MNO 4284) was shown by Boule (1929) to be representative of *Radulopecten inequicostatus.* To avoid confusion d'Orbigny's hypodigm was restricted to the specimen (l) which is clearly an example of *Ch. (Ch.) textoria.*

The figures of *'P.' peruanus* Tilmann, *'P.' pseudotextorius* Redlich; Borissiak and Ivanoff, *Ch. Meriani* (Greppin); Staesche (non Greppin), *'P.' (Ch.)* sp; Dietrich, *'Entolium'* (?) *Stoliczkai* (Gemmellaro); Lentini (non Gemmellaro), *Ch. ('Aequipecten')* cfr. *velata* (Golfuss); Lentini (non Goldfuss) all depict imperfectly preserved specimens in which neither the number of plicae nor the metric proportions could be accurately measured. However, except in the case of *'P.' peruanus* (where there is some resemblance to *Ch. (Ch.) valoniensis),* the overall form and disposition of the plicae leave little doubt that they should be included within *Ch. (Ch.) textoria.* Redlich's original description of *'P.' pseudotextorius* has yet to be traced.

The figures of *'P.' textorius* γ Quenstedt and *'P.' canaliculatus* Terquem and Piette depict fragmented specimens but the characteristic ornament of *Ch. (Ch.) textoria* is clearly visible.

The original description of *Ch. (Ch.) bedfordensis* Duff specifies, in contrast to *Ch. (Ch.) textoria,* different numbers of plicae on the right (70) and left (40) valves. However, it is not clear whether the description is based on a bivalved specimen and the holotype (OD; a right valve) of *Ch. (Ch.) bedfordensis* (BM LL27724) is very similar to small, finely ornamented specimens of *Ch. (Ch.) textoria.* Bearing in mind the great variability in the number of plicae in the latter species *Ch. (Ch.) bedfordensis* may well be synonymous.

The major proportion of the disc ornament in *Ch. (Ch.) wunschae* Marwick is very similar to *Ch. (Ch.) textoria* but the existence of what appears to be '*Camptonectes*-ornament' on the anterior and posterior dorsal margins probably serves to distinguish the species.

The specific name *articulatus* Schlotheim has frequently been applied (see Synonymy) to coarsely ornamented forms of *Ch. (Ch.) textoria* following the illustration of such a form under *'P.' articulatus* by Goldfuss (1833). However, v. Seebach (1864) and Cossmann (1911) have examined Schlotheim's type material and pronounced it to be representative of *P. vagans* J. de C. Sowerby (= *Radulopecten vagans).* Subsequent illustration of syntypes by Staesche (1926, pl. 1, figs. 10, 11) has confirmed distinctiveness from *Ch. (Ch.) textoria* (and thus the inappropriate use of the name by Goldfuss and later authors) although the affinities of the specimens seem to be with *R. inequicostatus.* v. Seebach considered that J. de C. Sowerby's specific name *vimineus* should be applied to forms like *'P.' articulatus* Goldfuss but de Loriol (1894) reckoned J. de C. Sowerby's species (from the Inferior Oolite [Cox and Arkell, 1948]) to be distinct from that of Goldfuss (from the Tithonian) and therefore created a new name *(nattheimiensis)* for the latter. Cossmann created *Ch. bathonica* for similar specimens from the Bathonian, reasoning apparently that mere stratigraphic separation merited a specific distinction. Oppel (1858) created *'P.' Dewalquei* for specimens referred to *'P.' articulatus* by Chapuis and Dewalque (1853) which he presumably considered to be outside Goldfuss' hypodigm for the species. The variety *Jurensis* Riche (1893) was created for forms with compound plicae and raised to specific rank by Rollier (1911). Since this feature is a common aspect of the variation in coarsely ornamented *Ch. (Ch.) textoria* (e. g. Pl. 7, Fig. 11), *'P.' (Ch.) jurensis* can safely be synonymised.

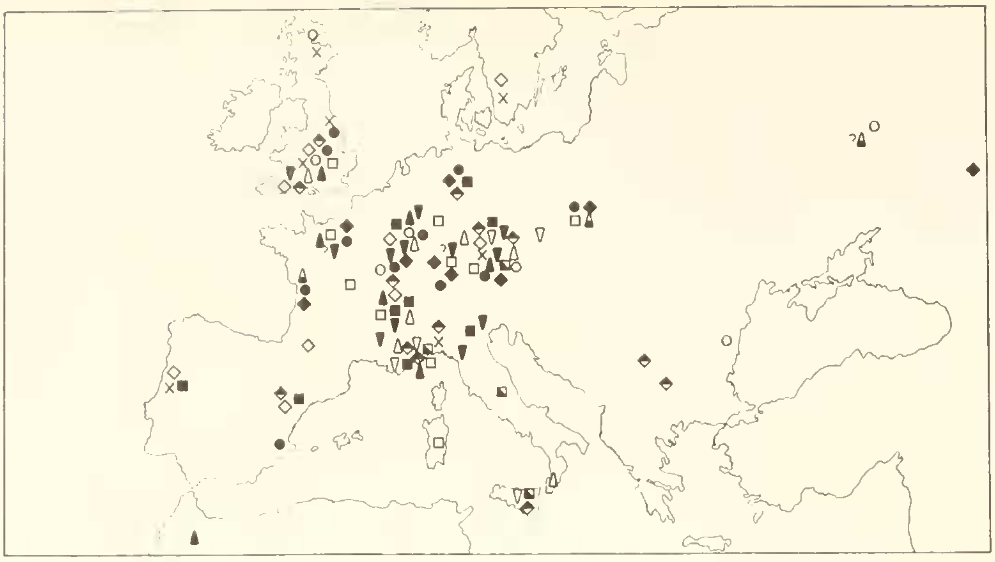
Rollier's species *'P.' (Ch.) protextorius, 'P.' (Ch.) Schombergensis, 'P.' (Ch.) Brisgoviensis, 'P.' (Ch.) Schlippei* and *'P.' (Ch.) Lycetti* were erected for specimens which he considered had been incorrectly assigned to synonyms of *Ch. (Ch.) textoria* by previous authors (respectively *'P.' textorius torulosi* Quenstedt, *'P.' textorius* Schlotheim; Quenstedt, *'P.' ambiguus* Münster; Schlippe, *'P.' Dewalquei* Oppel; Schlippe, *'P.' articulatus* Schlotheim; Lycett) but which are within the present author's hypodigm for *Ch. (Ch.) textoria.*

The affinities of *'P.' Palaemon* d'Orbigny, *'P.' dispar* Terquem, *'P.' textilis* Münster and *'P.' Trigeri* Oppel (and subsequent references thereto) are discussed under respectively, *Entolium (E.) lunare, Ch. (Ch.) valoniensis* and *Camptonectes (C.) subulatus* (last two).

In the interests of brevity secondary references to synonymous species are only listed in the synonymy where they occur in major works (e. g. Staesche, 1926, Dechaseaux, 1936) or where they are of relevance to the preceding discussed or sections 5–10. Further secondary references may be traced in Roemer (1839), Quenstedt (1843, 1852), d'Orbigny (1850), Bronn (1852), Oppel (1866), Laube (1867), Waagen (1867), Brauns (1871), Tate and Blake (1876), Lundgren (1881), Simpson (1884), Behrendsen (1891), Siemiradzki (1893), Bettoni (1900), Cossmann (1900), Trauth (1909), Simionescu (1910), Blaschke (1911), Rollier (1911), Cossmann (1919), Cox (1928), Vinassa de Regny (1933), Rakus (1964), Urlichs (1966), Barbulescu (1971) and Nitzopoulos (1974).

5. STRATIGRAPHIC RANGE

The earliest zonally defined records of *Ch. (Ch.) textoria* are from the Planorbis zone (Hettangian) of S. England (author's collection), the Rhone Basin (Dumortier, 1864), the Northern Alps (Neumayr, 1879) and Peru (Tilmann, 1917). Earlier records may however be constituted by occurrences in the 'Rhaeto-Lias' of E. France (Terquem, 1855) and N. Italy (Capellini, 1866). Apart from the above and records from the Angulata zone of S. England (BM 77247) and E. France (Terquem and Piette, 1865) the species is unknown until the Sinemurian when it becomes widespread and locally common. Numbers in the L. and U. Pliensbachian are perhaps somewhat reduced but the species remains widespread until the Toarcian. In the L. Toarcian *Ch. (Ch.) textoria* appears only to occur in any numbers in the Tenuicostatum zone of Luxembourg (Mauberge, 1851) and the Bifrons zone of the Lyonnais (Dumortier, 1874; Riaz, 1907; Roman, 1926). Certain U. Toarcian records are limited to specimens from the



Text fig. 156: *Chlamys (Ch.) textoria* – European distribution.

Cotswolds (BM L41990), E. Spain (BEHMEL and GEYER, 1966), Portugal (HALLAM, 1971), L. Saxony (ERNST, 1923) and Swabia (STAESCHE, 1926); the latter being the only area where the species occurs fairly frequently. Other Toarcian records in the literature (VERNEUIL and COLLOMB, 1952; J. MENEGHINI, 1881; BURCKHARDT, 1903; LANQUINE, 1929; DECHASEAUX, 1936) are from unspecified horizons within the stage and refer to indeterminate numbers of specimens. 'Toarcian' museum specimens, apart from those which are representative of the above records, are limited to three examples from Normandy (BM 65891, 65897, L38023) and one from Chile (BM LL26315).

In the Aalenian *Ch. (Ch.) textoria* again becomes locally common and continues thus through the Bajocian. In the Bathonian common occurrences are considerably more sparsely distributed and in the Callovian the species is only known to occur commonly at one horizon (Lamberti zone of Brora, Scotland). Apart from specimens from this locality undoubted examples of *Ch. (Ch.) textoria* from the Callovian in museums are limited to nine specimens from the E. Paris Basin (MNO [3], MNP [3], GPIT [2], DM) two from S. Germany (BSPHG, GPIG), two from Poland (BM LL17246-7) and two from England (SbM, OUM J4823). Bibliographic records excluding those which refer to the above specimens are limited to Russia (LAHUSEN, 1883; BORISSIAK and IVANOFF, 1917), Rumania (BARBULESCU, 1961), S. Germany (SCHLIPPE, 1888), the E. Paris Basin (DECHASEAUX, 1936), the Rhone Basin (LISSAJOUS, 1910, 1923) and England (DOUGLAS and ARKELL, 1928; COX and ARKELL, 1948) and the number of specimens in each case is probably small.

In the Oxfordian *Ch. (Ch.) textoria* again becomes locally common and continues thus until the U. Tithonian (BOEHM, 1883; REMES, 1903; KILIAN and GUEBHARD, 1905; YIN, 1931). However, distribution is at all times somewhat patchy.

6. GEOGRAPHIC RANGE

In the Lias *Ch. (Ch.) textoria* is known from a great many localities over a large area of Europe (text fig. 156) and at the same time it occurs widely in S. America (text fig. 157). The palaeolatitudinal range is thus about 100°. Since the species occurs in the Planorbis zone of both Europe and S. America migration to produce the disjunct distribution must have occurred either very early in the Jurassic or in the Triassic. The lack of direct shelf connections over this period would have forced *Ch. (Ch.) textoria* to use extremely long routes through either the Arctic or Antarctic regions if deep waters were to have been avoided. If the occurrence of specimens in the L. Jurassic outside Europe and S. America is at all indicative (by way of signifying the existence of populations which might be relicts) of the route taken, then the records of *Ch. (Ch.) textoria* from Japan and Siberia suggest that the Arctic route was adopted. However, the apparent absence of *Ch. (Ch.) textoria* from the L. Jurassic of western N. America (HAYAMI's [1961] record from N. America presumably referring to specimens collected from E. Greenland by ROSENKRANTZ [1934]) argues against this hypothesis and since MARWICK's (1953) single, doubtfully conspecific, specimen (see Section 4) is the only record from the L. Jurassic of Oceania the Antarctic route seems also to be precluded. The available evidence therefore suggests that *Ch. (Ch.) textoria* was able to migrate via the direct, deep water route of the Tethys and Pacific Oceans.

During the Toarcian *Ch. (Ch.) textoria* became much more sparsely distributed in Europe and outside the continent the species may well have been restricted to S. America.

During the Aalenian *Ch. (Ch.) textoria* was apparently confined to Europe where, however, it became more widespread although largely absent from the peri-Mediterranean region. A similar pattern of distribution was maintained throughout the rest of the Jurassic in Europe.

In the Bajocian the range extended along the southern shores of Tethys and apart from an apparent break in the Bathonian (which may be a function of collection failure) the species persisted in the latter area until the Kimmeridgian. WANDEL's (1936) single specimen from the Oxfordian of the E. Indies may indicate a similar spread along the northern shores of Tethys.

Text fig. 157: *Chlamys (Ch.) textoria* – World distribution (Callovian reconstruction).

The particular abundance of *Ch. (Ch.) textoria* in the Callovian of Cutch, India (Cox, 1952) in conjunction with the scarcity of the species in Europe (see Section 5) at this time suggests a shift in the centre of population, perhaps as a response to the widespread development of unfavourable bituminous shale facies (see Section 8) in the latter region.

In the Tithonian the range of *Ch. (Ch.) textoria* may well have contracted into Europe.

7. DESCRIPTION OF ECOLOGY

Rather than laboriously catalogue the particular variants of *Ch. (Ch.) textoria* present at a given locality the author has taken the liberty in the following description of referring specimens to one of three arbitrarily defined groups, characterised by the presence of 17–26 plicae, 27–36 plicae and more than 36 plicae at L: 20, known hereinafter as the 'coarse', 'intermediate' and 'fine' phenotypes respectively.

Ch. (Ch.) textoria first occurs in any numbers in the Sinemurian when however it is found widely in all the major facies developed in the stage. It is particularly common in the Arietenkalk (Bucklandi zone), a predominantly clay and micritic limestone sequence in S. W. Germany, where it reaches a maximum height of 53 mm (GPIT). All specimens in which the shell is preserved belong to the 'fine' phenotype. The species is also common in the stratigraphically slightly higher chamosite oolites of the Frodingham Ironstone (Semicostatum-Obtusum zones) where it reaches a maximum height of 37 mm (author's collection). The majority of specimens belong to the 'intermediate' phenotype but the 'fine' phenotype also occurs (assoc. fauna, p. 69). 'Fine' phenotypes constitute all the records of *Ch. (Ch.) textoria* from the U. Sinemurian Hierlatz Limestone of the N. Alps. Such phenotypes also form the basis for the many records of *Ch. (Ch.) textoria* from clays and micritic limestone in the L. Pliensbachian of S. W. Germany and the E. Paris Basin (where the species reaches a maximum height of 73.5 mm [Dechaseaux, 1936]). 'Intermediate' and 'coarse' phenotypes from this stage are restricted to two specimens from Germany (BSPHG; Pl. 7, Fig. 12) and one from Lorraine (NM).

Ch. (Ch.) textoria is widespread in the U. Pliensbachian but appears only to be common in micritic limestones in Swabia (Staesche, 1926) where it reaches a maximum height of 60 mm (BSPHG). No specimens are known from sandy facies in substage (e. g. Sandy Series, Yorkshire; Down Cliff and Thorncombe Sands, Dorset) and the species is rare in chamositic oolite facies (e. g. Cleveland and Banbury Ironstones) although it reaches a maximum height of 88 mm (BM 20166). In similar facies in the L. Toarcian of the Lyonnais the species is common but reaches a maximum height of only 36.5 mm (ENSM). 'Intermediate' phenotypes are more common than 'fine' but in argillaceous facies in the same substage in Luxembourg (Mauberge, 1951), *Ch. (Ch.) textoria* is represented only by 'fine' phenotypes (maximum height 35 mm [BSPHG]). All but one (GPIG) of the museum specimens examined by the author from argillaceous facies in the U. Toarcian of Swabia exhibit the 'fine' phenotype. The maximum height attained is 53.9 mm (Staesche, 1926). The associated benthic fauna is considerably reduced in density and somewhat reduced in diversity.

No specimens of *Ch. (Ch.) textoria* have been recorded from Toarcian bituminous shale deposits. An isolated specimen exhibiting the 'fine' phenotype (BM 65897; Pl. 8, Fig. 19) from the argillaceous sequence of Normandy is the largest (H: 73.5) known from the stage.

Although reef and reef-derived deposits are known in the Jurassic as early as the U. Pliensbachian (Jebel Bou-Dahar, Morocco [Dubar, 1948]) *Ch. (Ch.) textoria* delays its appearance in such facies until the Aalenian, when it is found commonly in the Pea Grit Coral Bed of the Cheltenham area in association with abundant limid bivalves, brachiopods, bryozoa and corals. All museum specimens which are undoubtedly derived from this horizon and locality exhibit the 'coarse' phenotype. The maximum height is 52 mm (BM L41973). The species is rare in Aalenian chamosite oolites in Britain (Northampton Sand Ironstone) and S. W. Germany but in Lorraine numerous specimens are recorded, reaching a maximum height of 65 mm (NM). 'Coarse' and 'intermediate' phenotypes are approximately equally represented.

In the Sauzei zone (L. Bajocian) of Malancourt Quarry, near Metz (E. Paris Basin), *Ch. (Ch.) textoria* occurs abundantly in a number of patch coral reefs and in the inter-reef biosparites and marls. In specimens collected by the author which are well enough preserved to allow plical counts to be made only one specimen of thirteen from the reef facies belongs to the 'intermediate' rather than the 'coarse' phenotype. Conversely, of ten specimens from the inter-reef facies only one belongs to the 'coarse' rather than the 'intermediate' phenotype. The maximum height of the author's specimens is 50 mm but a museum specimen (NM) from the same area and horizon has a height of 74.5 mm. The associated fauna in both reef and inter-reef facies is dominated by the bivalves *Ctenostreon*, *Lopha*, *Lucina*, *Pseudolimea* and *Trichites*, the brachiopods *Cymatorhynchia*, *Flabellirhynchia*, *Lobothyris* and *Rugitela*, the echinoids *Hemicidaris* and *Pseudodiadema*, the gastropod *Bourguetia* and serpulids and bryozoans. The coral genera *Isastrea* and *Thamnasteria* form the bulk of the reef masses (Hallam, 1975b).

In the roughly contemporaneous Sowerbyi-Banke, a marly oolite in S. W. Germany, *Ch. (Ch.) textoria* is common and reaches a maximum height of 57 mm (GPIG). Of the eighteen specimens from this bed in the GPIG, fifteen exhibit the 'intermediate' phenotype, two the 'coarse' and one the 'fine'. A shell bed of approximately the same age (Concavum-Discites zones) at Bradford Abbas, near Sherborne, Dorset has yielded numerous examples of the 'coarse' phenotype of *Ch. (Ch.) textoria* up to a maximum height of 38.5 mm (BM L11559). The associated benthic fauna is diverse and includes the bivalves *Trigonia* and *Astarte* together with the gastropods '*Alaria*', '*Cerithium*', '*Purpurina*' and '*Spinigera*' and the brachiopod '*Terebratula*' (Woodward, 1894).

In the U. Bajocian of the Cotswolds *Ch. (Ch.) textoria* is common in the Upper Coral Bed (Parkinsoni zone) in association with the reef-inhabiting pectinids *Spondylopecten (S.) palinurus* and *S. (S.) cardinatus*. Of the museum specimens which are certainly derived from this horizon only one (BM L41968) exhibits the 'intermediate' rather than the 'coarse' phenotype.

The 'coarse' phenotype of *Ch. (Ch.) textoria* is quite common (author's collection) in a coral bed in the M. Bathonian of the Carrière de Campagnettes (Normandy). The bivalves *Lithophaga*, *Plagiostoma*, *Trigonia* and *Vaugonia* and the brachiopod *Moorellina* make up the majority of the associated fauna (T. Palmer, 1974). A similar coral bed in Indre, where *S. (S.) palinurus* is an additional faunal element, also contains the 'coarse' phenotype of *Ch. (Ch.) textoria* (J.-C. Fischer, 1964).

In the U. Bathonian of Normandy the 'coarse' phenotype occurs quite commonly between sponge fronds in the reef-like structures exposed at St. Aubin. The maximum height is 50 mm (author's collection) and the most abundant elements of the associated fauna are the sponges *Platychonia* and *Limnoria*, the bivalve *Plagiostoma*, the brachiopod *Moorellina* and ectoprocts and serpulid worms (T. Palmer, 1974). *Ch. (Ch.) textoria* is rare outside coralliferous or spongiferous deposits in the Bathonian.

The only common occurrence of *Ch. (Ch.) textoria* in the Callovian is in the Clylenish Quarry Sandsone (Lamberti zone, E. Scotland) where the majority of specimens exhibit the 'intermediate' phenotype. The maximum height attained is 67 mm (BM L20601). Most of the remaining few Callovian records (see Section 5) seem also to be from arenaceous facies. However, specimens described by Duff (1978) from the bituminous shales of the L. Oxford Clay (Coronatum zone) in England (BM LL27724-8) may constitute a record of *Ch. (Ch.) textoria* ('fine' phenotype) from argillaceous facies (see Section 4). The maximum height of Duff's specimens is 9.7 mm.

In the Oxfordian, *Ch. (Ch.) textoria* is common in deposits of the Plicatilis zone in Oxfordshire and in Yorkshire, where the species reaches a maximum height of 82 mm (YM 570). According to Arkell (1931a) specimens from coral patch reefs generally exhibit the 'coarse' phenotype while those from inter-reef oolites and biosparites show the 'intermediate' phenotype. In the succeeding Transversarium zone deposits in Yorkshire (Coral Rag), examples of the 'coarse' phenotype (author's collection) are associated with almost in situ corals at Whitewall Corner Quarry, near Malton (assoc. fauna p. 157). In the Ringstead Coral Bed (Pseudocordata zone) both 'coarse' and 'intermediate' phenotypes are found but the former become relatively more common to the east, paralleling an increase in the abundance of corals (Fürsich, 1976). There are no records of *Ch. (Ch.) textoria* from the Oxfordian part of the Oxford Clay.

The 'coarse' phenotype is quite common in the Oxfordian coral reefs developed in the Swiss Jura (de Loriol, 1893) and the Yonne (MNP, assoc. fauna, p. 88). At least in the latter area specimens exhibiting the 'fine' phenotype (reaching a maximum height of 46 mm [MNP]) are also quite common in non-reef biomicrites. The 'intermediate' phenotype is absent from both areas.

Ch. (Ch.) textoria does not appear to be common elsewhere in the Oxfordian.

In the marly limestones of the Baden Beds (Kimmeridgian) in the Swiss Jura 'intermediate' phenotypes of *Ch. (Ch.) textoria* are quite common (de Loriol, 1878). Only seven of the nineteen museum specimens (GPIT [14], GPIG [4], BSPHG) which are undoubtedly derived from similar facies in the U. Jurassic of the Swabian Jura exhibit this phenotype (H_{max}: 39, GPIT). The remainder is made up of specimens displaying the 'fine' phenotype (H_{max}: 36, BSPHG). Both the 'intermediate' (Dollfus, 1863) and 'coarse' (de Loriol and Pellat, 1875) phenotypes are recorded from clays in the Kimmeridgian of the Boulonnais but the numbers are indeterminate and probably small.

Ch. (Ch.) textoria is recorded from Kimmeridgian coralliferous facies in Franconia (Boehm, 1881a) and the Jura (Contejean, 1859; Thurmann and Étallon, 1862) but is unknown at La Rochelle. In the L. Tithonian reef complex at Neuburg (assoc. fauna, p. 88) the species is common (Yamani, 1975). 'Coarse' and 'intermediate' phenotypes appear to be about equally frequent but the 'fine' phenotype is represented by only two specimens. By contrast,of the eleven museum specimens (GPIT [9], BSPHG [2]) derived from L. Tithonian reef complexes elsewhere in S. Germany fully six exhibit the 'fine' phenotype. The remainder is made up of three 'coarse' and two 'intermediate' phenotypes. Gemmellaro and Di Blasi (1874) record seven specimens of *Ch. (Ch.) textoria* from contemporaneous coralliferous facies in Sicily of which six exhibit the 'coarse' and one the 'intermediate' phenotype. Boehm (1883) records 60 representatives of the 'coarse' phenotype from U. Tithonian reef limestones at Stramberg. Only one example of the 'intermediate' (BSPHG) and none of the 'fine' phenotype are known from this horizon and locality. In other Tithonian reef facies in Languedoc (Yin, 1931) and the Maritime Alps (Kilian and Guébhard, 1905) *Ch. (Ch.) textoria* is represented solely by the 'coarse' phenotype. However in Isère (Faure-Marguerit, 1920) the 'fine' phenotype seems also to be present.

Staesche (1926) reports common examples of the 'coarse' phenotype from the Brenztaloolith, an oolite passing laterally into coral/*Diceras* facies in the L. Tithonian of S. W. Germany. A single specimen from the 'Portlandian' of the Yonne (Dechaseaux, 1936) is the only record of *Ch. (Ch.) textoria* from any horizon in the Jurassic where the associated fauna (in this case an abundance of *Cyrena* and *Corbula* [Arkell, 1956]) is indicative of reduced salinity.

8. INTERPRETATION OF ECOLOGY

The strong correlation, apparent from Section 7, between the occurrence of the 'coarse', 'intermediate' and 'fine' phenotypes and the existence of respectively reefs, non-reefal arenites and argillaceous sediments is the basis for considering that the majority of the variation exhibited by Group 3 (p. 161) is ecophenotypic and is concordant with the view that all members of Group 3 belong to the same species, *Ch. (Ch. textoria.* The lack of a strict phenotype facies correspondence does not necessarily weaken the grounds for this dual hypothesis since there is no reason to suppose that the boundaries of the phenotypes, arbitrarily defined at the outset, should agree perforce with the limits of variation in each facies.

The relatively large number of 'intermediate' phenotypes at Neuburg may merely reflect the development of inter-reef arenites while the high proportion of 'fine' phenotypes from other reef complexes in S. Germany may simply reflect the development of inter-reef argillites. It is also not unreasonable to suggest that the numerous examples of the 'coarse' phenotype in the Brenztaloolith are derived from nearby reefs. However, derivation from reefs is an implausible explanation for the high proportion of 'coarse' phenotypes in the Aalenian of Lorraine. The nearest reefs are apparently some 250 km away, in Nièvre (Arkell, 1956). Furthermore the exclusive occurrence of the 'coarse' phenotype in the Bradford Abbas Fossil Bed is not matched by the presence of a reef-derived fauna. Similarly there is no evidence of nearby sand-grade sediments to explain the exclusive occurrence of the 'intermediate' phenotype in the Baden Beds. It may be however that some environmental variable which is itself only loosely related to sedimentary facies is the real determinant of the phenotype adopted by *Ch. (Ch.) textoria*. Thus, until such time as their environments are more fully characterised and shown to be indistingushable from those of sediments containing the 'normal' phenotype for the facies, these few exceptions imply no need to assume that morphology is not controlled by the environment nor do they require rejection of the single species hypthesis advanced on p. 161.

An example illustrating the need for detailed facies analysis is provided by the reef-like stuctures at St. Aubin, colonised by examples of *Ch. (Ch.) textoria* exhibiting the 'coarse' phenotype. The vertical elongation of the sponge masses suggests that an upstanding framework existed and since such was undoubtedly the case in most coral accumulations containing the 'coarse' phenotype it is tempting to attribute the development of the 'coarse' phenotype to this factor. However, closer analysis of the sediments at St. Aubin indicates that the sponge masses had a relief of no more than a few centimetres above the sea bed and that their vertically elongated shape is the result of upward growth to keep pace with sedimentation (T. J. Palmer, pers. comm., 1978; see also T. Palmer and Fürsich [1981]). It therefore seems more likely that the development of the 'coarse' phenotype is due to growth in a partially enclosed habitat (see Section 9). This explanation incidentally also obviates the need to make the assumption, implicit thus far but possibly invalid in the cases of the Ringstead and Campagnettes Coral Beds, that coral accumulations which themselves had little palaeo-relief but which contain the 'coarse' phenotype of *Ch. (Ch.) textoria* were derived from unexposed structures of genuine reefal dimensions.

The fact that in roughly contemporaneous samples from each of the Sinemurian and Toarcian, individuals with the 'fine' phenotype attain a larger size than those with the intermediate phenotype, provides strong support for the view (see p. 163) that variation in the number of plicae is an adaptive result of developmental flexibility. Tho only case where stunting may yet be invoked is for the very small, finely ornamented and questionably conspecific specimens from the L. Oxford Clay. Here the small size and low diversity of the associated benthic faunal elements (Duff, 1975) suggests that conditions were unfavourable for growth, probably as a result of low oxygen tension.

The absence of *Ch. (Ch.) textoria* from deep water pelagic limestones in the M. and U. Jurassic of the peri-Mediterranean region indicates that soupy substrates were not acceptable. However, the occurrence of the species in the U. Toarcian of Swabia, where the reduced density and diversity of the benthic fauna is probably the result of sediment instability, signifies at least some tolerance in this direction.

Apart from restrictions imposed by soft substrates, low oxygen tension and reduced salinities *Ch. (Ch.) textoria* seems to have been a remarkably eurytopic species. However, facies which were colonised at one time were not always occupied at another.

The absence of the species from reefal facies in the U. Pliensbachian of Morocco may perhaps be explained by competitive inferiority to the essentially Tethyan bivalves *Pseudopecten (Ps.) dentatus*, *Ps. (Ps.) veyrasensis*, *Lithiotis* and *Pachyrisma* which occur there.

The invocation of competitive inferiority, in this case to *Radulopecten vagans* and *R. fibrosus*, also goes a long way towards explaining the localised distribution of *Ch. (Ch.) textoria* in suitable shallow water facies at later horizons in the Jurassic. The rarity of the species in anything but coralliferous and spongiferous deposits in the Bathonian is matched by a corresponding abundance of *R. vagans* while the rarity of *Ch. (Ch.) textoria* in Callovian sands and L. Oxfordian biosparites in Yorkshire, some M. Oxfordian oolites and biosparites in Oxfordshire, and in the M. and U. substages of the Oxfordian in Dorset is paralleled by the frequent occurrence of *R. fibrosus*. However, the restricted occurrence of *Ch. (Ch.) textoria* in U. Jurassic argillaceous sediments, which contrasts markedly with its even distribution in such facies in the Lias, is not readily explicable by a competitive reaction and seems to imply an evolutionary reduction in tolerance. It is tempting to relate this to the species population size bottle-neck which must have accompanied the reduction in geographic range and patchy distribution of *Ch. (Ch.) textoria* in the Toarcian and Aalenian (see Sections 5, 6).

The rarity of the species in U. Pliensbachian ironstones in England and similar facies in the Aalenian of England and Germany cannot be explained by competitive inferiority or an evolutionary reduction in tolerance since almost identical sediments with a comparable fauna in the Sinemurian of England and the Toarcian and Aalenian of France contain numerous examples of *Ch. (Ch.) textoria*. Neither can these factors be invoked to account for the absence of the species from U. Pliensbachian sands in England since comparable facies were colonised by the species in the Sinemurian and Callovian. At present no alternative explanation for these anomalous absences is available. Likewise no plausible explanation can be offered for the lack of *Ch. (Ch.) textoria* in coral patch reefs at La Rochelle. An appeal to the exceptionally high density of these reefs, such as has been made to account for the corresponding rarity of the reef-inhabiting species *Spondylopecten subspinosus* (see p. 88) is ruled out by the fact that *Ch. (Ch.) textoria* occurs abundantly in similarly dense structures at Malancourt.

Disregarding those times when the lack of a particular phenotype is merely the result of the inability of *Ch. (Ch.) textoria* to colonise the relevant facies (see above) the rarity of the 'coarse' phenotype in the L. Jurassic and Callovian, of the 'intermediate' phenotype in the L. Pliensbachian and of the 'fine' phenotype in the M. Jurassic can be attributed to the poor development of respectively 'reefs', non-reefal arenites and argillaceous sediments at these times. The lack of the 'intermediate' phenotype in the Oxfordian of the Yonne has yet to be explained. Appropriate facies were apparently well developed (Mégnien et al., 1970).

9. FUNCTIONAL MORPHOLOGY

The moderate to large byssal notch of *Ch. (Ch.) textoria* indicates that the species was byssally attached for at least the earlier parts of ontogeny. The maximum height of 93.5 mm (GPIT 2-92-3) in the 'coarse' phenotype is comparable to that in the close morphological analogue *Gloripallium pallium*, a Recent species which remains byssate beneath coral heads throughout ontogeny (Waller, 1972b). The maximum height of 80 mm (YM 570) attained by the 'intermediate' phenotype is not approached by any Recent morphological analogue although *Ch. varia*, an ecological analogue, is known to reach a height of 63.5 mm (Tebble, 1966) and to remain byssate throughout ontogeny (Soemodihardjo, 1974). The maximum height of 73.5 mm in the 'fine' phenotype is exceeded by the Recent morphological analogue. *Ch. islandica* (Wiborg, 1963) but it is not clear whether byssal attachment is maintained at these sizes.

The reduced convexity and ornament of the right valve in *Ch. (Ch.) textoria* is paradigmatic for tight fixation during at least some periods in life.

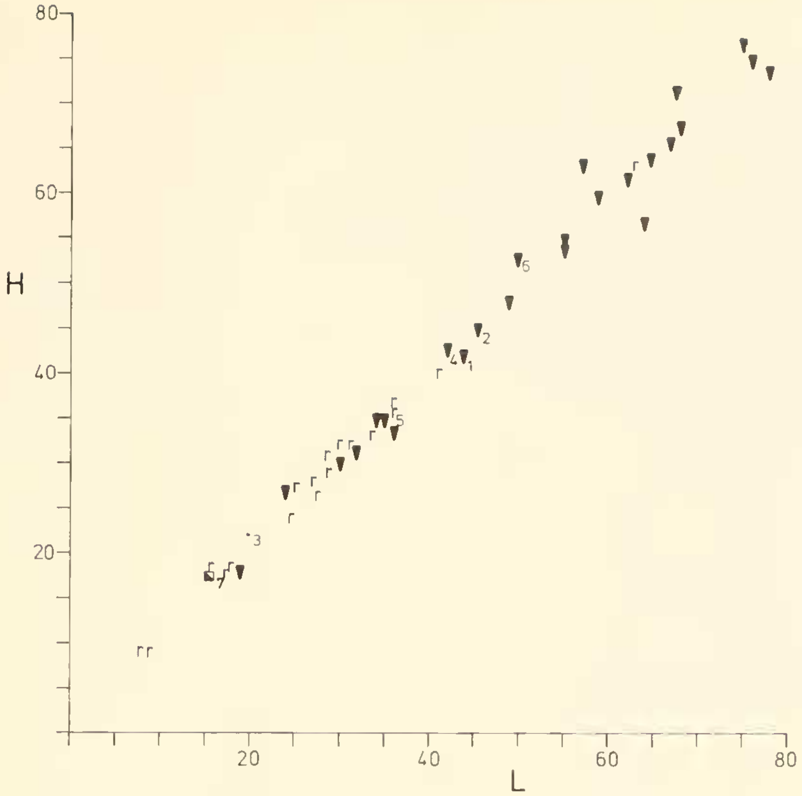
All three of the above analogues are reported to be capable of swimming although *Ch. islandica* seems to be more proficient than the others.

The larger plical amlitudes of *Ch. (Ch.) textoria* in organic build-ups almost certainly conferred greater strength on the shell and may therfore have been developed as part of a 'siege' policy towards predators. The more strongly developed comarginal lamellae on the left valve could have contributed to such a policy by gripping the substrate and preventing extraction from crevice type microhabitats, in much the same way as short spines prevent extraction of the Recent species *Ch. dieffenbachi* from sponges (Beu, 1966). The low plical amplitudes, smaller comarginal lamellae and lower H/UA ratios of *Ch. (Ch.) textoria* in argillaceous sediments would have increased streamling and thrust/weight ratio, and hence swimming ability, and may therefore have been developed in line with a 'fugitive' policy towards predators. It is however difficult to account in these terms for the development of an intermediate morphology in arenaceous facies save as a means of facilitating a joint 'siege'/'fugitive' policy. Indeed, while detracting from a 'fugitive' policy, the relatively large comarginal lamellae of forms from arenaceous compared to argillaceous facies could have done nothing to enhance a 'siege' policy in the lack of an enclosed habitat. Moreover there is no a priori reason, except perhaps in the case of organic build-ups, why different policies towards predators should have been adopted in each facies. A completely different order of explanation for the relationship between phenotype and facies in *Ch. (Ch.) textoria* may therefore be required. Camouflage, relating to the 'grainsize' of the substrate, seems the most likely alternative.

10. ORIGINS AND EVOLUTION

Since *Ch. (Ch.) textoria* is known from the lowest zone in the Jurassic its origins probably lie in the Triassic. Two specimens (BM unnumbered; L705, Pl. 8, Fig. 4) from the Muschelkalk of S.W. Germany appear to be within the phenotypic range of *Ch. (Ch.) textoria* and may therefore indicate that the species was in existence in the M. Triassic. Staesche (1926) has suggested that *Ch. reticulata* (Schlotheim), a species from the same horizon, may have been the ancestor while Dechaseaux (1936) has proposed *'Pecten' tenuistriatus* Münster for the same role. The latter author cites two species from the Cretaceous, *Ch. Goldfussi* (Deshayes) and *Ch. Archiaciana* (d'Orbigny), as possible descendants of *Ch. (Ch.) textoria*.

Maximum height appears to undergo a random oscillation from the Sinemurian (53 mm) to the L. Pliensbachian (73.5 mm) to the U. Pliensbachian (88 mm) to the Toarcian (73.5 mm) to the Aalenian (62 mm) to the Bajocian (74.5 mm) to the Bathonian (50 mm) to the Callovian (67 mm) to the Oxfordian (82 mm) to the Kimmeridgian (72 mm; Dollfus, 1863) to the Tithonian (93.5 mm); GPIT 2-92-3).



Text fig. 158: *Chlamys (Ch.) valoniensis* – height/length.

Chlamys (Chlamys) valoniensis (Defrance 1825b)
Pl. 9, Figs. 1–6; text figs. 158–166

Synonymy

1825b	*Pecten Valoniensis* sp. nov; Defrance, p. 507, pl. 22, fig. 6.
? 1838	*Pecten lugdunensis* sp. nov; Michelin in Leymerie, p. 346, pl. 24, fig. 5.
1838	*Pecten Valoniensis* Defrance; Leymerie, p. 368, pl. 24, fig. 6.
?pv* 1851	*Pecten acutauritus* sp. nov; Schafhautl, p. 416, pl. 7, fig. 10.
? 1855	*Pecten dispar* sp. nov; Terquem, p. 323, pl. 23, fig. 6.
v* 1858	*Pecten cloacinus* sp. nov; Quenstedt, p. 31, pl. 1, figs. 33, 34.
v*? 1858	*Pecten disparilis* sp. nov; Quenstedt, p. 47, pl. 4, figs. 8, 9.
1860	*Pecten Falgeri* Merian; Stoppani, p. 76, pl. 14, fig. 3.
? 1860	*Pecten janiriformis* sp. nov; Stoppani, p. 76, pl. 14, figs. 4–6.
? 1860	*Pecten aviculoides* sp. nov; Stoppani, p. 77, pl. 14, fig. 7.
? 1860	*Pecten barnensis* sp. nov; Stoppani, p. 78, pl. 15, fig. 2.
? 1860	*Pecten Winkleri* sp. nov; Stoppani, p. 78, pl. 15, fig. 4.
1864	*Pecten valoniensis* Defrance; Dumortier, p. 58, pl. 9, figs. 1–6, pl. 10, figs. 1–3.
(?) 1865	*Pecten dispar* Terquem; Terquem and Piette, p. 103.
(?) 1865	*Pecten lugdunensis* Michelin; Terquem and Piette, p. 104.
1866	*Pecten Falgeri* Merian; Capellini, p. 479, pl. 5, figs. 14–19.
? 1866	*Pecten aviculoides* Stoppani; Capellini, p. 480, pl. 5, figs. 20–23.
? 1866	*Pecten janiriformis* Stoppani; Capellini, p. 480, pl. 6, figs. 1–3.
v*? 1866	*Pecten Etheridgii* sp. nov; Tawney, p. 81, pl. 3, fig. 4.
v* 1866	*Pecten Suttonensis* sp. nov; Tawney, p. 81, pl. 3, fig. 3.
1868	*Pecten valoniensis* Defrance; Jaubert, p. 260.
1878	*Pecten (Chlamys) Uhligi* sp. nov; Gemmellaro and Di Blasi in Gemmellaro, p. 394, pl. 30, figs. 8, 10.
1886	*Pecten valoniensis* Defrance; Winkler, p. 31.
1903	*Pecten (Chlamys) valoniensis* Defrance; Bistram, p. 36, pl. 3, fig. 3.
1903	*Pecten (Chlamys) dispar* Terquem; Bistram, p. 36, pl. 3, fig. 3.
? 1903	*Pecten (Chlamys) Falgeri* Merian; Bistram, p. 37, pl. 3, fig. 1.
(?) 1904	*Chlamys* cf. *dispar* (Terquem); Cossmann, p. 504.
1905	*Pecten valoniensis* Defrance; H. Allen, p. 172.
1907	*Pecten (Chlamys) valoniensis* Defrance; Joly, p. 24.
(?) 1907	*Pecten (Chlamys) dispar* Terquem; Joly, p. 75.
1909	*Pecten (Chlamys) Valoniensis* Defrance; Trauth, p. 91.
1925	*Pecten* cf. *valoniensis* Defrance; Dubar, p. 257.
v 1926	*Chlamys acutaurita* (Schafhautl); Staesche, p. 27, pl. 2, fig. 4.
1926	*Chlamys valoniensis* Defrance; Roman, p. 105.
1929	*Pecten (Chlamys) valoniensis* Defrance; Lanquine, p. 60.
1929	*Pecten (Chlamys) janiriformis* Stoppani; Lanquine, p. 60, pl. 1, fig. 4.
(?) 1929	*Pecten (Chlamys) Falgeri* Merian; Lanquine, p. 60.

1936 *Pecten (Chlamys) Valoniensis* DEFRANCE; DECHASEAUX, p. 27.

(?) 1936 *Pecten (Chlamys) dispar* TERQUEM; DECHASEAUX, p. 27.

1945 *Chlamys valoniensis* (DEFRANCE); VECCHIA, p. 6.

(?) 1945 *Chlamys falgeri* (MERIAN); VECCHIA, p. 7.

1950 *Chlamys valoniensis* (DEFRANCE); ROMAN, p. 25.

? 1951 *Pecten* sp; TROEDSSON, p. 140.

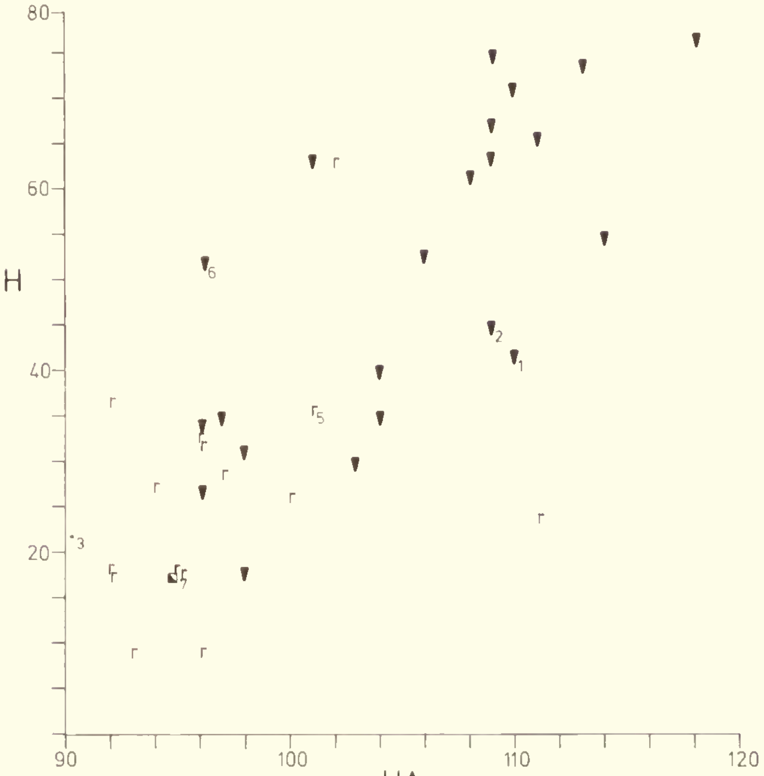
1953 *Chlamys valoniensis* (DEFRANCE); MOUTERDE, pp. 311, 313, 337.

1968 *Chlamys valoniensis* (DEFRANCE); WOBBER, p. 306.

1973 *Chlamys (Chlamys) dispar* (TERQUEM); LENTINI, p. 24, pl. 14, figs. 8, 9, ?pl. 14, fig. 10; pl. 15, figs. 1, 2, 4, 5.

1975 *Pecten acuteauritus* SCHÄFHAUTL; MORBEY, text fig. 2.

The type material of *Pecten Valoniensis* DEFRANCE 1825b, p. 507, pl. 22, fig. 6 (originally housed in Caen, France) was destroyed in the Second World War. Mr. P. HODGES (University College of Swansea) has obtained topotype material from the Calcaire de Valognes (Hettangian) of Normandy with the intention of designating a neotype.



Text fig. 159: *Chlamys (Ch.) valoniensis* – height/umbonal angle.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

None given.

2. DIAGNOSIS

Distinguished from both *Ch. (Ch.) pollux* and *Ch. (Ch.) textoria* by the lack of ornament on the plicae.

3. DESCRIPTION

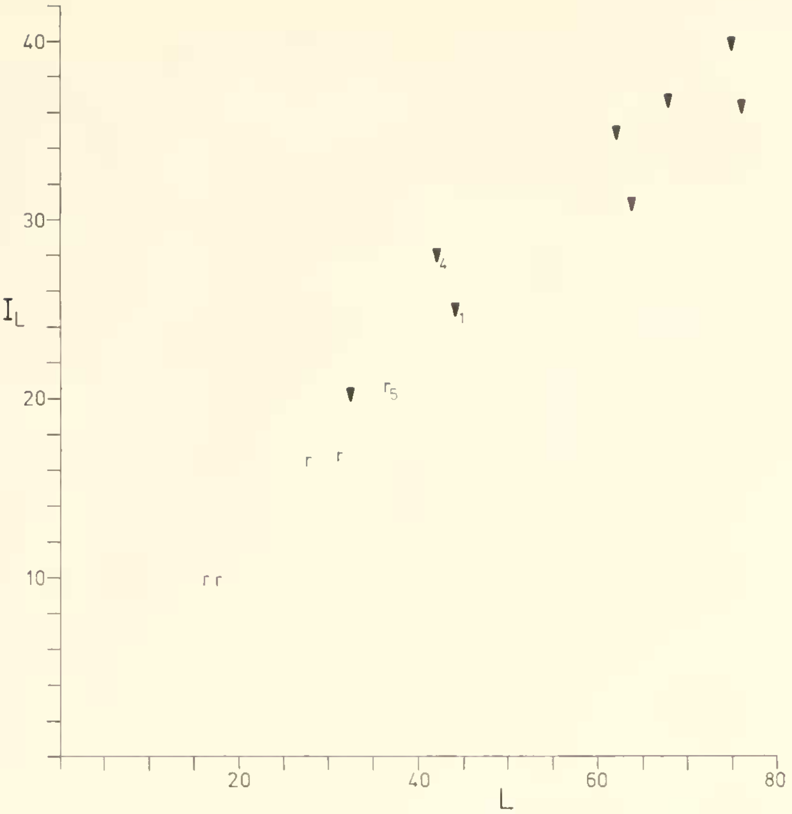
Disc sub-ovate, higher than long, early in ontogeny, becoming sub-orbicular (text fig. 158) near maximum height of 77 mm (ENSM). Umbonal angle variable (text fig. 159), increasing during ontogeny to produce slightly concave dorsal margins. Disc flanks moderately high and ornamented with vertical striae.

Slightly inequilateral, posterior sector somewhat larger; inequivalve, left valve moderately convex, right valve almost flat.

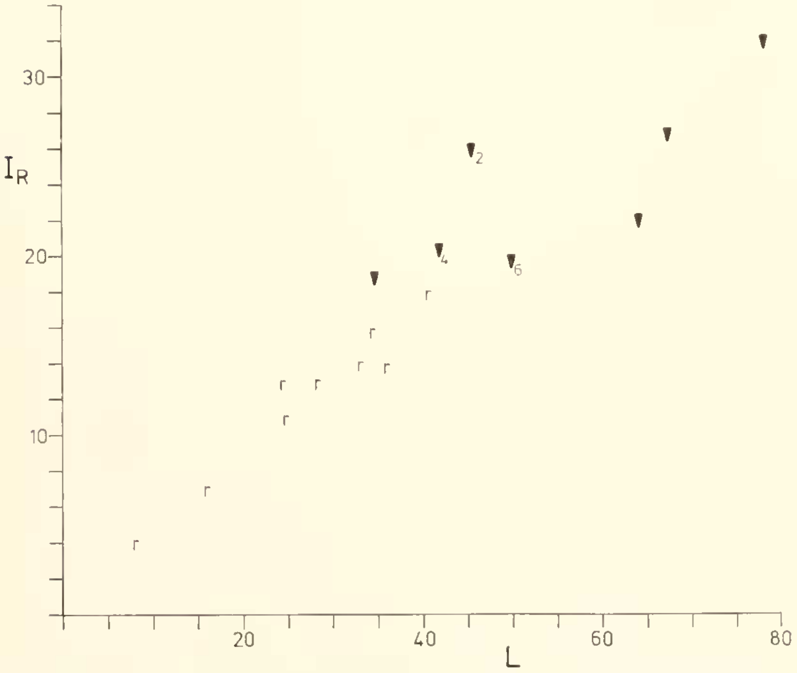
Intersinal distance greater in left valve than right, increasing at a decreasing rate in both (text figs. 160, 161). Depth of byssal notch variable, moderate to large (text fig. 162).

Auricles well demarcated from disc, approximately equal in size. Anterior auricles meeting hinge line at an acute angle; posterior auricles meeting hinge line at an obtuse angle. Anterior auricle of right valve meeting disc at an acute or right angle; remaining auricles meeting disc at an acute angle. Anterior auricles bearing 4–6 radial costae.

Height of anterior auricle and lengh of anterior hinge increasing at a markedly decreasing rate (text figs. 163, 164). Length of posterior hinge increasing with similar but less marked allometry (text fig. 165).



Text fig. 160: *Chlamys (Ch.) valoniensis* – intersinal distance on left valve/length.



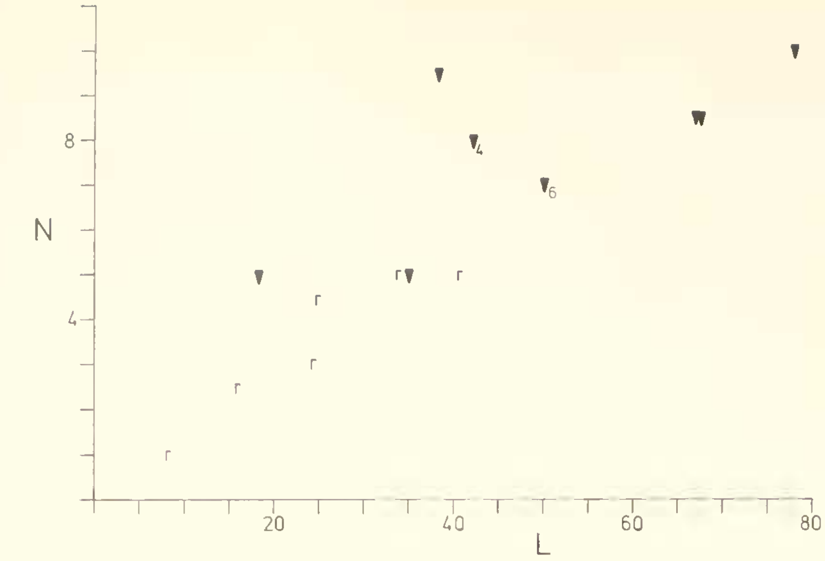
Text fig. 161: *Chlamys (Ch.) valoniensis* – intersinal distance on right valve/length.

Both valves bearing a variable number of radial plicae (Pl. 9, figs. 1–6), increasing in number by intercalation from between 20 and 30 early in ontogeny. Right valve with 31–36 at L: 20, about 39 at L: 40, about 49 at L: 60, up to a maximum of 52 at L: 67.5 (ENSM). Left valve with 36–45 at L: 20, 44–65 at L: 40, 52–72 at L: 60, up to a maximum of 79 at L: 68 (ENSM).

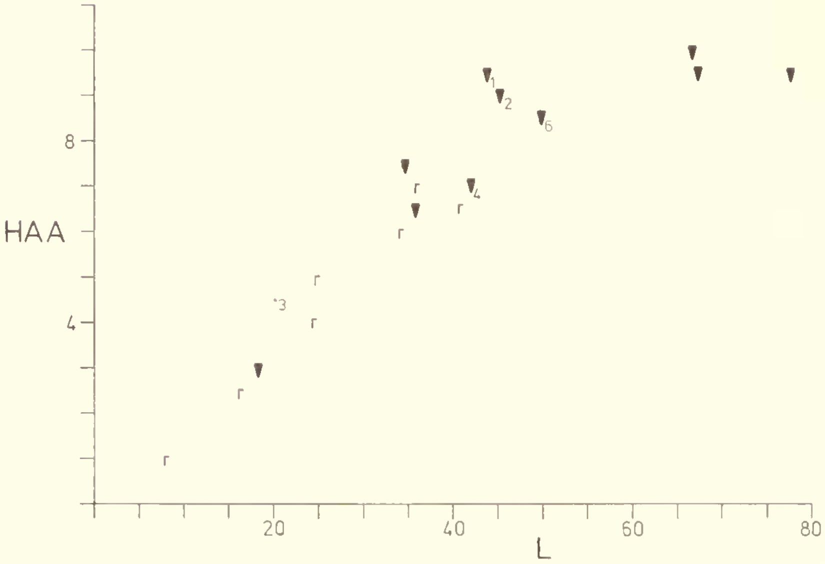
Shell thickness moderate.

4. DISCUSSION

The original figure of '*Pecten*' *Valoniensis* DEFRANCE is a poor reproduction of an internal view of a left valve. Metric proportions (1) plot within the range of the species described in Section 3 and LEYMERIE (1838) and DUMORTIER (1864), both French authors who may have had access to the type material, have applied the name to figured specimens which undoubtedly belong to the latter species. Bearing this in mind and the



Text fig. 162: *Chlamys (Ch.) valoniensis* – depth of byssal notch/length.



Text fig. 163: *Chlamys (Ch.) valoniensis* – height of anterior auricle/length.

fact that the horizon of derivation (Calcaire de Valognes) is one from which numerous examples of the species described in Section 3 have been recovered (see Section 7), Defrance's name can be confidently applied as senior synonym to the latter species, despite the lack of diagnostic features in the original figure. Mr. P. Hodges will shortly be designating a neotype (see above).

The original figure of '*P.*' *lugdunensis* Michelin is very reminiscent of *Pseudopecten (Ps.) equivalvis* (q. v.). However, Dumortier (1864), who appears to have examined the type material, has stated that Michelin's species is in fact equivalent to *Ch. (Ch.) valoniensis* and this view has been taken by later authors (e. g. Staesche, 1926) who may also have examined the type material. The anomalously low number of plicae in the right valve (25 at L: 45.5) and the high I_R/L (2) of the original figure in comparison to *Ch. (Ch.) valoniensis* might be the result of respectively, preservation as an internal mould and inaccurate illustration. In view of the somewhat equivocal position of Michelin's species, Terquem and Piette's (1865) unillustrated record of '*P.*' *lugdunensis* can only tentatively be placed in synonymy.

The original figure of '*P.*' *acutauritus* Schafhautl seems to depict an abraded specimen of *Ch. (Ch.) valoniensis* and what is apparently one of Schafhautl's syntypes (BSPHG; AS IX 42; Pl. 9, Fig. 3) undoubtedly belongs to the latter species. Metric proportions of the original figure (3) are inseparable from *Ch. (Ch.) valoniensis*.

The original figure of '*P.*' *dispar* Terquem depicts a right valve with 41 plicae at L: 42 which has resemblances to both *Ch. (Ch.) valoniensis* and *Ch. (Ch.) textoria*. The specimen referred to Terquem's species by Bistram (1903) undoubtedly belongs in *Ch. (Ch.) valoniensis* and all but one (pl. 14, fig. 10, which has imbricate lamellae and is thus closer to *Ch. (Ch.) textoria*) of Lentini's (1973) examples of *Ch. (Ch.) dispar* are similarly referable. However, in view of the fact that Terquem's original figure has an abnormally high I_L/L and

AH/L (4) some doubt must remain as to his hypodigm until the type material is located. With the possibility of confusion unillustrated records of Terquem's species in Terquem and Piette (1865), Cossmann (1904), Joly (1907) and Dechaseaux (1936) can only tentatively be placed in synonymy.

It has proved impossible to trace the original reference to *'P.' Falgeri* Merian. Specimens figured under this name by Stoppani (1860) and Capellini (1866) are clearly representative of *Ch. (Ch.) valoniensis* but Bistram's (1903) figure bears some resemblance to *Pseudopecten (Ps.) equivalvis.* It is not clear which, if any, of these authors has examined the type material so the position of Merian's species is uncertain. Consequently unfigured records of his species in Lanquine (1929) and Vecchia (1945) can only be provisionally synonymised.

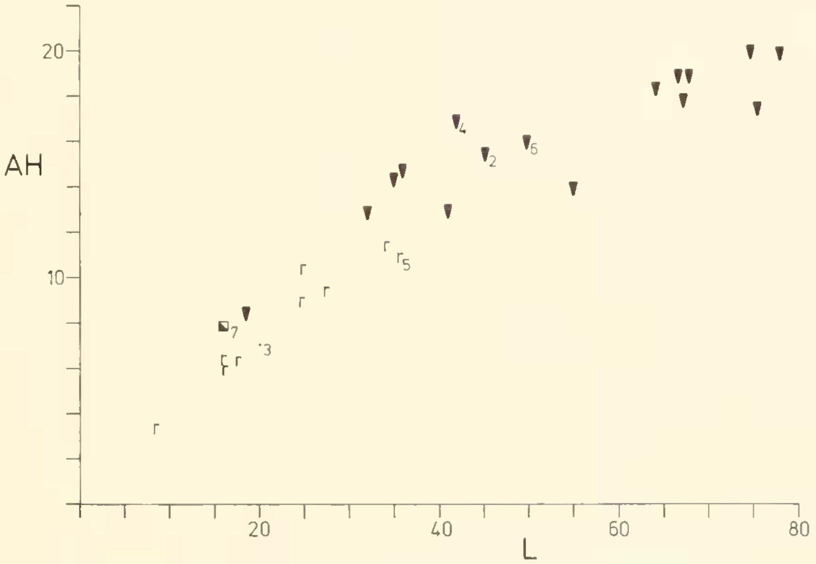
The position of *'P.' janiriformis* Stoppani is also in doubt. Although the original figure is available and resembles *Ch. (Ch.) valoniensis,* Capellini (1866), who worked in the same field area (N. Italy) as Stoppani and who may have examined the latter's type material, has applied his specific name to specimens which are closer to *Ch. (Ch.) textoria.* Whether or not they correspond to the original hypodigm for *'P.' janiriformis,* specimens referred to this species by Lanquine (1929) undoubtedly fall within the present author's concept of *Ch. (Ch.) valoniensis.*

Capellini has also applied *'P.' aviculoides* Stoppani, a species founded on a fragment resembling *Ch. (Ch.) valoniensis,* to a specimen which has closer affinities with *Ch. (Ch.) textoria.* With this uncertainty over the position of Stoppani's species *'P.' barnensis* and *'P.' Winkleri,* both of which show similarities to *Ch. (Ch.) valoniensis,* are best treated as only provisional synonyms.

The sole observed syntype of *'P.' cloacinus* Quenstedt (GPIT 2-1-33; Pl. 9, Fig. 5) is indistinguishable from *Ch. (Ch.) valoniensis* by the number of plicae on the left valve (44 at L: 36) and by metric proportions (5). The number of plicae in *'P.' Suttonensis* Tawney (sole observed type, IGS 7830; Pl. 9, Fig. 4) and *'P.' Uhligi* Gemmellaro and Di Blasi has not been measured but appears to be within the range of *Ch. (Ch.) valoniensis* of comparable size. Metric proportions (6 and 7 respectively) are indistinguishable from the latter species.

'P.' sp.; Troedsson was compared with *Ch. (Ch.) valoniensis* and in view of the horizon of derivation (Rhaetic) it seems very likely to be a representative of this species.

The affinities of *'P.' disparilis* Quenstedt and *'P.' Etheridgii* Tawney are discussed under *Camptonectes (C.) subulatus.*

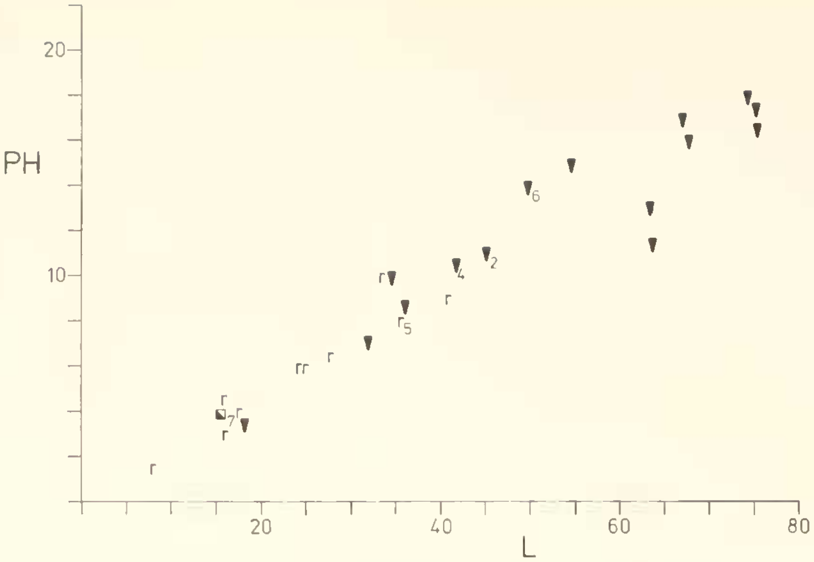


Text fig. 164: *Chlamys (Ch.) valoniensis* – anterior hinge length/length.

5. STRATIGRAPHIC RANGE

Ch. (Ch.) valoniensis is first recorded from the L. Rhaetic Westbury Formation of Glamorgan and Gloucestershire, where it is common. In the U. Rhaetic Lilstock Formation of the same area it is rare but records from the 'Rhaetic' of Lombardy (Stoppani, 1860), Spezia (BM L14938), Provence (Lanquine, 1929), the Pyrenees (Dubar, 1925), Belgium (Joly, 1907) and Swabia (GPIG, GPIT) may include specimens from equivalent horizons as also may records from the 'Rhaeto-Lias' of Spezia (Capellini, 1866) and Lombardy (Vecchia, 1945). The species occurs almost throughout the type section of the Rhaetian in the Kendelbach Gorge, Austria (Morbey, 1975).

In the Jurassic *Ch. (Ch.) valoniensis* is known from the Planorbis zone (Hettangian) in the Rhone Basin (Dumortier, 1864; Roman, 1926), N. Italy (Bistram, 1903) and S. Wales (Wobber, 1968). 'Hettangian' records from S. France (Leymerie, 1838; Jaubert, 1868; Roman, 1950), E. France (Dechaseaux, 1936) and N. W. France (Defrance, 1825b) probably also stem from this zone. The species is known from the Angulata zone of Bavaria (Winkler, 1886) but specimens recorded by Terquem and Piette (1865) from this horizon and from the Sinemurian in E. France are only possibly conspecific (see Section 4). There is however no reason to doubt the conspecific status of at least some of the specimens recorded by Dechaseaux (1936) from the Sinemurian of Lorraine. Since the latter is the latest stage-defined record of *Ch.*



Text fig. 165: *Chlamys (Ch.) valoniensis* – posterior hinge length/length.

(Ch.) valoniensis it is doubtful whether 'L. Lias' records in GEMMELLARO (1878) and TRAUTH (1909) include any specimens from the L. Pliensbachian.

6. GEOGRAPHIC RANGE

Ch. (Ch.) valoniensis occurs widely in Europe (text fig. 166) but elsewhere is known only from one questionably conspecific specimen (BM L72864) from Iran.

7. DESCRIPTION OF ECOLOGY

In the Westbury Formation (L. Rhaetic) *Ch. (Ch.) valoniensis* occurs most abundantly in thin limestones containing numerous examples of the bivalves *Rhaetavicula contorta* and *Placunopsis alpina*. It is however also found in carbonaceous and pyritous shales containing, in addition to *R. contorta* and *Pla. alpina*, *Eotrapezium*, *Lyriomorphia*, *Protocardia*, *Tutcheria* and the gastropod '*Natica*' (IVIMEY-COOK, 1974). Ammonites are absent throughout the formation and brachiopods, bryozoa, crinoids and corals are rare. In the overlying Lilstock Formation, where *Ch. (Ch.) valoniensis* is rare (D. JONES, pers. comm., 1978) the fauna is even more reduced in diversity with *Liostrea*, *Modiolus* and *Plagiostoma* the only important molluscan elements.

The number of specimens involved in other Rhaetic records is not clear but the species may well be common in N. Italy (see Sections 4, 5). The maximum height attained in the Rhaetic is 63.5 mm (BM 50031).

In the Hettangian of Glamorgan *Ch. (Ch.) valoniensis* is common in nearshore lithoclast sands containing numerous bryozoa, brachiopods, and corals but few ammonites (WOBBER, 1968). The species also occurs in thin clay interbeds but passing eastwards into a continuous offshore argillaceous sequence containing a more diverse ammonite and bivalve fauna, it becomes progressively rarer.

Text fig. 166: *Chlamys (Ch.) valoniensis* – European distribution.

Ch. (Ch.) valoniensis is common in the Gresten Beds (L. Lias, Austria); littoral sands, shales and limestones bordering the Palaeozoic massif of Bohemia and containing numerous examples of *Ch. (Ch.) textoria* and *Pseudopecten* (Trauth, 1909). The species also occurs commonly (H_{max}: 77, ENSM) in the Calcaire de Valognes (Hettangian, Normandy) which may represent a similar littoral facies developed at the margins of the Brittany massif. *Ch. (Ch.) pollux* is an associated faunal element (Dumortier, 1864).

Dechaseaux (1936) reports numerous examples of *Ch. (Ch.) valoniensis* from nearshore sands in the Hettangian of Lorraine.

The species is not known to be common elsewhere in the L. Lias but the number of records from the Hettangian of S. France (see Section 5) suggests that it is by no means rare in the latter region. The stage is usually developed in limestones and marls overlying the Palaeozoic basement. *Ch. (Ch.) pollux* and *Pseudopecten* are also recorded (Roman, 1950; Mouterde, 1953).

There are no records from the Hettangian of Portugal where the reduced diversity bivalve fauna (dominated by *Isocyprina* and mytilids) is indicative of abnormal salinity (Böhm, 1901). Similar facies in the Hettangian of N. W. Germany are also lacking in *Ch. (Ch.) valoniensis* (Huckriede, 1967).

8. INTERPRETATION OF ECOLOGY

It is apparent from Section 7 that *Ch. (Ch.) valoniensis* favoured nearshore environments although in such situations both clay-grade and sand-grade substrates were colonised. Anaerobic conditions (pyritic and carbonaceous horizons in the Westbury Formation) were apparently tolerable but markedly abnormal salinities (Lilstock Formation; Hettangian of Portugal and N. W. Germany) were not. The reduced diversity fauna of the Westbury Formation may be indicative of slightly reduced salinity (D. Jones, pers. comm., 1978) so the common occurrence of *Ch. (Ch.) valoniensis* could imply a measure of euryhalinity. However the absence of at least ammonites could merely be due to the shallow water depositional environment thus eurytopy in *Ch. (Ch.) valoniensis* may extend no further than a tolerance of a variety of fully marine nearshore situations.

The fact that in the Westbury Formation *Ch. (Ch.) valoniensis* occurs most abundantly at horizons with the lowest faunal diversity is suggestive of an opportunistic adaptive strategy (Levinton, 1970).

Co-occurrence of *Ch. (Ch.) valoniensis* and the closely related species *Ch. (Ch.) pollux* indicates that even if there was any tendency for the species to compete, it was suppressed by niche partitioning. The latter may have been effected by the use of different byssal attachment sites (see Section 9 and p. 187).

9. FUNCTIONAL MORPHOLOGY

The moderate to large byssal notch and low convexity right valve of *Ch. (Ch.) valoniensis* are adaptive for tight byssal fixation. However ontogenetic decrease in the relative length of the anterior auricle would have progressively reduced the efficiency of the byssus so it is doubtful whether the species could have remained attached in the adult stage.

The great majority of extant byssally attached pectinids apply the byssus to a hard substrate and there is no reason to suppose (cf. *Ch. (Ch.) pollux*) that *Ch. (Ch.) valoniensis* differed from this practice.

The relatively greater convexity of the left valve in *Ch. (Ch.) valoniensis* is paradigmatic for swimming. Ontogenetic increase in the umbonal angle probably served to maintain efficient swimming in the adult stage.

Intercalation of plicae is paradigmatic for the maintenance of shell strength and stiffness with increasing size. However, in view of the fact that many much larger pectinids do not exhibit plical intercalation it must be doubted whether this was its sole function in *Ch. (Ch.) valoniensis*.

10. ORIGINS AND EVOLUTION

No obvious ancestors for *Ch. (Ch.) valoniensis* present themselves in the Triassic.

Within the species there appear to be no phyletic trends apart from an increase in maximum height from the Rhaetic (63.5 mm) to the Hettangian (77 mm).

The post-Planorbis zone decline of *Ch. (Ch.) valoniensis* is approximately correlated with the rise of *Ch. (Ch.) textoria* and *Pseudopecten*. However, the possibility of a causal connection in terms of competition is rendered unlikely by the fact of the co-occurrence of the former with each of the latter.

Chlamys (Chlamys) pollux (d'Orbigny 1850)

Pl. 9, Figs. 7, 8; text fig. 167

Synonymy

v* 1850	*Pecten Pollux* sp. nov; d'Orbigny, v. 1, p. 220 (Boule, 1907, v. 2, p. 267, pl. 23, figs. 16, 17).
1864	*Pecten Pollux* d'Orbigny; Dumortier, p. 65, pl. 10, figs. 11, 12, pl. 11, figs. 1–4.
1876	*Pecten pollux* d'Orbigny; Tate and Blake, p. 362.
1891	*Pecten amphiarotus* sp. nov; Di Stefano, p. 62.
1894	*Pecten pollux* d'Orbigny; Woodward, p. 360.
non 1909	*Pecten amphiarotus* Di Stefano; Trauth, p. 90, pl. 2, fig. 17.
1936	*Aequipecten pollux* (d'Orbigny); Dechaseaux, p. 41.
1950	*Chlamys Pollux* (d'Orbigny); Roman, p. 25.
1953	*Pecten pollux* d'Orbigny; Mouterde, p. 311.
? 1973	*Chlamys (Aequipecten) amalthea* (Oppel); Lentini, p. 27, pl. 15, fig. 9 (non Oppel sp.).
1973	*Chlamys (Aequipecten)* cfr. *Pollux* (d'Orbigny); Lentini, p. 27, pl. 16, fig. 1.

Lectotype of *Pecten Pollux* d'Orbigny 1850, v. 1, p. 220 designated herein; MNS 1591; figured Boule, 1907, pl. 23, fig. 16; H: 35, L: 31, I_R: 17, N: 4, AH: 12, PH: 9, HAA: 7, PL: 24; Sinemurian, Pouilly (Côte d'Or). Paralectotype; MNS 1591A; figured Boule, 1907, pl. 23, fig. 17; also Sinemurian, Pouilly.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

'Très-belle expèce à grosses côtes inégales, dont quelques-unes sont porvues de très-longues pointes tubuleuses. Au-dessous de l'*O. arcuata*, à Pouilly (Côte d'Or).'

2. AMENDED DIAGNOSIS

Distinguished from both *Ch. (Ch.) textoria* and *Ch. (Ch.) valoniensis* by the presence of long tubular spines.

3. AMENDED DESCRIPTION

Shape essentially similar to *Ch. (Ch.) valoniensis*. Differing only by the somewhat larger H/UA, by the slight ontogenetic reduction in the relative size of the byssal notch and by the tendency for the anterior auricles to meet the hinge line at a right angle.

Both valves ornamented with between 22 and 27 (usually 24) rounded radial plicae. Those on right valve low, equal in size, and up to 50% bearing tubular spines up to 5 mm in length, set at intervals of about 5 mm (Pl. 9, Fig. 7). Those on left valve markedly unequal in size, 5–7 being larger and bearing robust tubular spines up to 10 mm in length, spaced at intervals of about 10 mm (Pl. 9, Fig. 8). Spines absent from both valves at shell heights below about 10 mm. Sulci equal in width to plicae; both traversed by closely spaced fine comarginal striae.

Hinge line of right valve bearing dorsally directed spines up to 5 mm in length, spaced at intervals of 2–3 mm.

Shell thickness moderate. Maximum height 53 mm (BM L65791).

4. DISCUSSION

The two syntypes of *'Pecten' Pollux* D'ORBIGNY are both right valves, one of which (MNS 1591) is well preserved while the other (MNS 1591A) is somewhat abraded. The former is herein designated as lectotype. Although brief, D'ORBIGNY's (1850) diagnosis and description could refer to no Sinemurian pectinid other than the species described in Section 3. There is consequently no doubt that the first taxonomically valid use of *'P.' pollux* was in 1850 (see ICZN Opinion 126) and that therefore D'ORBIGNY's species is the senior synonym for the species described in Section 3.

DI STEFANO (1891) provided no illustration of *'P.' amphiarotus* but mention in the description of spines and unequal plicae leaves little doubt that the species (from the L. Lias) is synonymous with *Ch. (Ch.) pollux*. TRAUTH's (1909) misapplication of DI STEFANO's specific name is discussed under *Pseudopecten (Ps.) dentatus*.

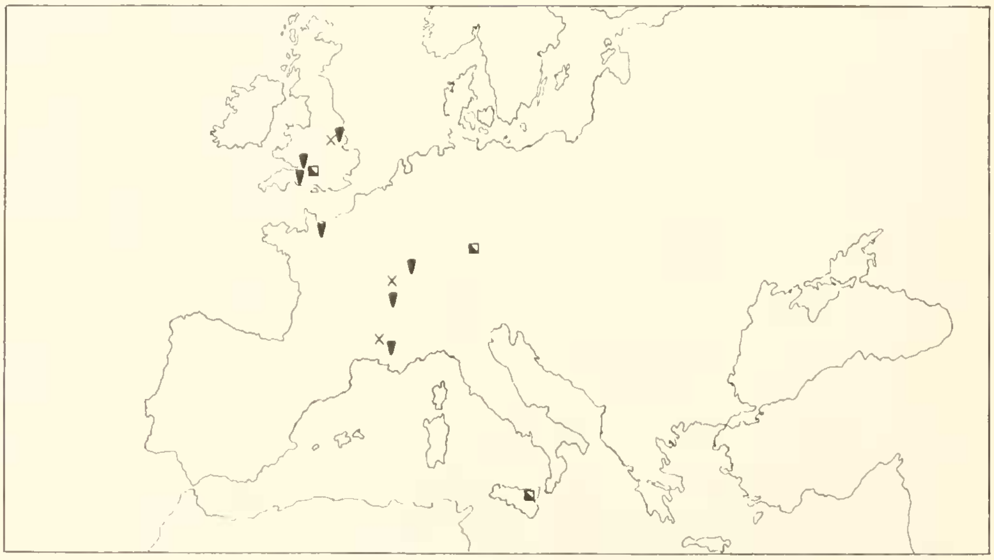
Since LENTINI (1973) referred to 22 'ribs' in his description of *Ch. ('Aequipecten') amalthea* (OPPEL) his use of this specific name is undoubtedly outside OPPEL's (1858) hypodigm (= *Propeamussium (P.) pumilum*). The figured specimen (from the L. Lias) appears to exhibit abraded spines and therefore may well be conspecific with *Ch. (Ch.) pollux*.

5. STRATIGRAPHIC RANGE

A few specimens of *Ch. (Ch.) pollux* are known from the uppermost Trias of the N. Calcareous Alps (BSPHG). In Britain the earliest records of *Ch. (Ch.) pollux* are from the White Lias (≡ pre Planorbis beds, lowermost Hettangian sensu POOLE [1979]) of the Bristol area (BM L74405, L77279, L77312, L77313, L78402).

In Planorbis zone deposits *Ch. (Ch.) pollux* is known from a number of localities in England (TATE and BLAKE, 1876; WOODWARD, 1894) and is reported to be common in the Rhone Basin (DUMORTIER, 1864).

ROMAN (1950) reports common examples of *Ch. (Ch.) pollux* from undifferentiated Hettangian in the Rhone Basin and DUMORTIER (1864), MOUTERDE (1953) and DECHASEAUX (1936) refer to indeterminate numbers of 'Hettangian' specimens from respectively Normandy, the Rhone Basin and the E. Paris Basin.



Text fig. 167: *Chlamys (Ch.) pollux* – European distribution.

Sinemurian records are limited to seven specimens from the Rhone Basin (ENSM [5]; MNS 1591, 1591A) and indeterminate numbers of specimens from the Bucklandi zone of England (Woodward, 1894).

It is very doubtful whether 'L. Lias' specimens of *Ch. (Ch.) pollux* (BM L1548; BSPHG; Di Stefano, 1891; ?Lentini, 1973) are derived from horizons higher than the Sinemurian.

6. GEOGRAPHIC RANGE

Ch. (Ch.) pollux is unknown outside Europe. Within Europe the species occurs over a broad latitudinal range (text fig. 167) but is only known to be common in the Rhone Basin (Dumortier, 1864; Roman, 1950) and Sicily (Di Stefano, 1891). This suggests a preference for warm waters (however see Section 8).

7. DESCRIPTION OF ECOLOGY

The common examples of *Ch. (Ch.) pollux* reported by Roman (1950) from the Hettangian of the Rhone are derived from marls containing the bivalves *Ch. (Ch.) valoniensis*, *Pseudopecten (Ps.) dentatus*, *Plicatula*, *Plagiostoma* and *Cardinia* together with crinoids and corals.

Specimens from the White Lias of the Bristol area (see Section 5) are derived from fine grained limestones and are sometimes associated with crinoid debris (e. g. BM L77279).

8. INTERPRETATION OF ECOLOGY

The limited available data suggests that *Ch. (Ch.) pollux* preferred low energy environments. The apparent rarity of the species in sediments indicative of such environments in N. Europe may be due to a dislike for relatively cool waters (see Section 6). It may however equally well be a consequence of the relative rarity of an, as yet unidentified, commensal organism (see Section 9).

The co-occurrence of *Ch. (Ch.) pollux* and the probable ancestor, *Ch. (Ch.) valoniensis* (also see p. 185), suggests that any competitive tendencies which the species may have had were suppressed by niche partitioning (see Section 10).

9. FUNCTIONAL MORPHOLOGY

The moderate to large byssal notch and only moderate adult size (H_{max}: 53) of *Ch. (Ch.) pollux* suggest that the species was byssally attached through most, if not all, of ontogeny. The low convexity of the right valve suggests that *Ch. (Ch.) pollux* was tightly fixed. The existence of spines on the right valve is non-paradigmatic for such a mode of life on hard substrates but is adaptive (providing additional purchase) for tight fixation on soft substrates. Since spines on the right valve and a large byssal notch are present in *Ch. dieffenbachi*, a Recent species which lives within sponges (Beu, 1966) it may be that *Ch. (Ch.) pollux* was tightly attached to this or some other group of soft bodied organisms.

The spinose ornament on the right valve of *Ch. (Ch.) pollux* almost certainly did not act as an adaptation for a late ontogenetic reclining phase either in the form of an anchor or as a device to prevent sinking into the sediment (see p. 83). The low environmental energy and fairly firm substrates indicated by respectively, argillaceous sediments and a diverse associated epifauna, would have created no need for either of the above adaptations. Spines on the left valve could have served no useful purpose for reclining in either of the above contexts.

10. ORIGINS AND EVOLUTION

Ch. (Ch.) pollux is almost certainly a descendant of *Ch. (Ch.) valoniensis* from which it differs significantly only by the reduced number of plicae and the presence of spinose ornament. Since the adult number of plicae in *Ch. (Ch.) pollux* is roughly equivalent to the juvenile number in *Ch. (Ch.) valoniensis*, *Ch. (Ch.) pollux* may be neotenous with respect to this character. The evolution of spinose ornament cannot be explained by heterochrony in the absence of ancestral allometry and suggests therefore that speciation may well have infolved changes in the structural genome as well as the regulatory changes implied by neoteny.

Since *Ch. (Ch.) pollux* appears to arise within the geographic range of *Ch. (Ch.) valoniensis* the possibility of sympatric speciation cannot be ruled out. However, since there is no evidence that *Ch. (Ch.) valoniensis* ever attached itself to the soft-bodied organisms to which *Ch. (Ch.) pollux* was presumable restricted (see p. 185 and Section 9), the author can propose no means by which such sympatric speciation might have been effected (cf. *Camptonectes (Camptochlamys) clathratus*).

Within *Ch. (Ch.) pollux* the detection of any definite phyletic changes in morphology is precluded by the paucity of specimens available for study. Maximum height may undergo a decrease in the passage from the Hettangian (53 mm; BM L65791) to the Sinemurian (35 mm; MNS 1591).

Apart from the extinction of a host organism (see Section 9) no plausible deterministic explanation is available to account for the post-Sinemurian extinction of *Ch. (Ch.) pollux*.

Genus *RADULOPECTEN* Rollier 1911

Type species. OD; Rollier 1911, p. 158; *Pecten hemicostatus* Morris and Lycett 1853, p. 10, pl. 1, fig. 16; Great Oolite (Bathonian), Minchinhampton, Gloucestershire.

DIAGNOSIS

Between 4 and 15 initial radial plicae, bearing comarginal lamellae at all stages of ontogeny on left valve but only in later stages of ontogeny or not at all on right valve.

Stratigraphic range; Jurassic (Aalenian-Tithonian). Geographic range; Europe, Asia, Africa, ?North and Central America.

DISCUSSION

Since all the Jurassic pectinid species which come under the Treatise definition of *Chlamys* (see p. 161) but which do not belong to *Ch. (Chlamys)* seem to form a monophyletic group they are usefully accorded a generic distinction from *Chlamys*. The name *Radulopecten* has been previously applied at the subgeneric level (e. g. ARKELL, 1931a; COX, 1952; DUFF, 1978) to certain members of this group and it is herein adopted, with a revised diagnosis (see above), as the generic name for the complete group.

Within *Radulopecten* seven groups may be distinguished on the following basis:

1. Left valve lacking plicae early in ontogeny but bearing about 25 radial striae of which initially between 4 and 14 develop into equal sized plicae (= *R. vagans*).
2. Left valve lacking plicae early in ontogeny but bearing about 40 radial striae of which initially about 15 develop into equal sized plicae (= *R. varians*).
3. Left valve lacking plicae early in ontogeny but bearing between 60 and 75 radial striae of which usually between 5 and 8 develop into equal sized plicae (= *R. strictus*).
4. Plicae present at earliest ontogenetic stages, increasing in number by intercalation. Usually one less plica on right valve than left; latter bearing between 10 and 13 equal sized originals (= *R. fibrosus*).
5. Plicae present at earliest ontogenetic stages, increasing in number by intercalation and accompanied by radial striae. Usually one more plica on right valve than left; latter bearing between 8 and 11 equal sized originals (= *R. scarburgensis*).
6. Plicae present at earliest ontogenetic stages, rarely increasing in number by intercalation. 11 equal sized original plicae on left valve, 12 on right; ornamented with conical spines (= *R. sigmaringensis*).
7. Plicae arising early in ontogeny. Between 5 and 9 unequal initial plicae, rarely increasing in number by intercalation but accompanied by radial striae (= *R. inequicostatus*).

Since the stratigraphic ranges of Groups 1 and 2 have little or no overlap it is conceivable that the supposed evolution of the latter from the former occurred without splitting. However since the morphological distance between the groups is quite large and there appear to be no intermediates, the groups are treated as separate lineages for reasons of convenience. Similar reasoning applies to the separation of the undoubtedly related Groups 5 and 6.

Groups 4, 5 and 7 tend to be restricted to particular facies (respectively; arenaceous, argillaceous and coralliferous) and since there is considerable overlap in their ranges of variation it may be that they represent ecophenotypes of a single species as has been suggested for similarly facies-restricted forms assigned to *Chlamys (Ch.) textoria*. However, unlike the latter species, the features distinguishing the groups would have to have resulted from very early ontogenetic developmental flexibility. Since the author can envisage no way of testing for such developmental flexibility it seems preferable to treat the groups as separate species. In any case, at least for Groups 4 and 5, there are considerable differences in geographic distribution which are difficult to relate to facies and each group is occasionally found in the facies apparently appropriate to the other, so it is perhaps more likely that they represent separate species. Similar reasoning applies to Groups 2 and 3 where, for example, BUVIGNIER's (1852) records suggest some morphological overlap.

Notable differences in the mean form of the ornament between the latest and earliest populations of Group 4 are attributed to phyletic evolution within a single species since there can be no doubt of direct relationship and there is no convincing evidence of the contemporaneous existence of two separate lineages (see p. 207). The latest (uppermost Oxfordian and Kimmeridgian) populations are characterised by the development of a larger umbonal angle (specimens marked with a glyph in text fig. 187) but this is clearly a simple reflection of the attainment of greater size.

Differences in the mean form of the ornament between earlier and later populations in Groups 1 and 5 can also be interpreted as the result of phyletic evolution within single species. Since however in Group 1 the difference in mean form results from a change in the relative proportions of two distinct ('striate' and 'non-striate') morphs there is here the possibility that the difference reflects a shift in the relative abundances of two quite separate species (see p. 192 for a refutation of this argument).

Radulopecten vagans (J. DE C. SOWERBY 1826a)

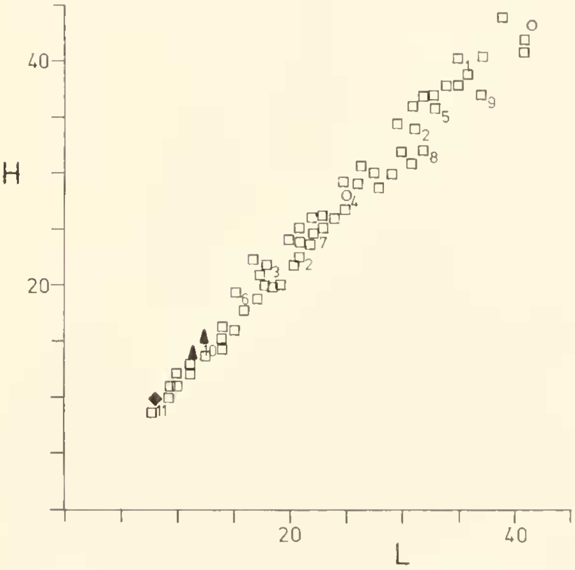
Pl. 9, Figs. 9–33, ?Fig. 34; text figs. 168–176

Synonymy

v* 1826a *Pecten vagans* sp. nov; J. DE C. SOWERBY, p. 82, pl. 543, figs. 3, 4, 5.
non 1833 *Pecten vagans* J. DE C. SOWERBY; GOLDFUSS, p. 44, pl. 89, fig. 8.
? 1839 *Pecten vagans* J. DE C. SOWERBY; ROEMER, p. 29.
1839 *Pecten vagans* J. DE C. SOWERBY; BEAN, p. 60.
v* 1850 *Pecten Rhetus* sp. nov; D'ORBIGNY, v. 1, p. 314 (BOULE, 1912, v. 7, p. 92, pl. 2, fig. 20).
v*p 1850 *Lima Nerina* sp. nov; D'ORBIGNY, v. 1, p. 313 (BOULE, 1912, v. 7, p. 92, pl. 2, figs. 21, 22).
v 1850 *Pecten vagans* J. DE C. SOWERBY; D'ORBIGNY, v. 1, p. 314.
1852 *Pecten anisopleurus* sp. nov; BUVIGNIER, p. 23, pl. 19, figs. 31–35.
1852 *Pecten fibrosus* J. SOWERBY; QUENSTEDT, p. 507, pl. 40, fig. 43 (non J. SOWERBY sp.).
1853 *Pecten vagans* J. DE C. SOWERBY; MORRIS and LYCETT, p. 8, pl. 1, figs. 12, 12a.
v* 1853 *Pecten peregrinus* sp. nov; MORRIS and LYCETT, p. 9, pl. 1, fig. 14.
v* 1853 *Pecten hemicostatus* sp. nov; MORRIS and LYCETT, p. 10, pl. 1, fig. 16.
1858 *Pecten vagans* J. DE C. SOWERBY; OPPEL, p. 491.
1858 *Pecten hemicostatus* MORRIS and LYCETT; OPPEL, p. 491.
? 1859 *Pecten Thurmanni* sp. nov; CONTEJEAN, p. 315, pl. 23, figs. 10–12.
1860 *Pecten vagans* J. DE C. SOWERBY; COQUAND, p. 68.
non 1860 *Pecten vagans* J. DE C. SOWERBY; DAMON, pl. 9, fig. 4.
v* 1863 *Pecten Griesbachi* sp. nov; LYCETT, p. 31, pl. 33, figs. 6, 6a.
1863 *Pecten inaequicostatus* PHILLIPS; LYCETT, p. 32, pl. 33, fig. 1a (non fig. 1; non PHILLIPS sp.).
v* 1863 *Pecten Rushdenensis* sp. nov; LYCETT, p. 33, pl. 33, figs. 4, 4a–c.
v* 1863 *Pecten Wollastonensis* sp. nov; LYCETT, p. 33, pl. 33, figs. 2, 2a–c.
1863 *Pecten anisopleurus* BUVIGNIER; LYCETT, p. 33, pl. 33, figs. 5, 5a.
1867 *Pecten vagans* J. DE C. SOWERBY; LAUBE, p. 10, pl. 1, fig. 10.

1867 *Pecten hemicostatus* Morris and Lycett; Laube, p. 11, pl. 1, fig. 15.
1869 *Pecten hemicostatus* Morris and Lycett; Terquem and Jourdy, p. 127.
1869 *Pecten anomalus* sp. nov; Terquem and Jourdy, p. 128, pl. 13, figs. 18–20, 20a.
1869 *Pecten rushdenensis* Lycett; Terquem and Jourdy, p. 129.
non 1880 *Pecten vagans* J. de C. Sowerby; Damon, pl. 9, fig. 4.
v* 1883 *Pectes intermittens* sp. nov; Whidborne, p. 500, pl. 15, figs. 13, 13a.
? 1886a *Pecten samilus* sp. nov; De Gregorio, p. 669, pl. 1, fig. 7.
? 1886c *Pecten eglus* sp. nov; De Gregorio, p. 10, pl. 4, figs. 13a, 13b.
1888 *Pecten vagans* J. de C. Sowerby; Schlippe, p. 131, pl. 2, fig. 5.
1888 *Pecten hemicostatus* Morris and Lycett; Schlippe, p. 133, pl. 2, fig. 8.
1898 *Pecten hemicostatus* Morris and Lycett; Greppin, p. 128.
1900 *Aequipecten fibrosus* (J. Sowerby); E. Philippi, p. 98, text fig. 15 (non J. Sowerby sp.).
1906 *Chlamys semicostata* sp. nov; Cossmann, p. 3, pl. 1, figs. 6, 7, pl. 2, fig. 22.
1906 *Chlamys rosimon* (d'Orbigny); Cossmann, p. 4, pl. 1, figs. 7–9 (non d'Orbigny sp.).
1910 *Chlamys vagans* (J. de C. Sowerby); Lissajous, p. 360, pl. 9, fig. 8.
1911 *Pecten (Radulopecten) hemicostatus* Morris and Lycett; Rollier, p. 158.
v 1916 *Pecten* cf. *anomalus* Terquem and Jourdy; Paris and Richardson, p. 533, pl. 45, figs. 1a–d.
v 1916 *Pecten vagans* J. de C. Sowerby; Paris and Richardson, p. 533.
non 1917 *Pecten vagans* J. de C. Sowerby; Borissiak and Ivanoff, p. 33, pl. 4, fig. 6.
1917 *Pecten hemicostata* Morris and Lycett; Borissiak and Ivanoff, p. 35, pl. 4, figs. 1–5, 10, 11.
1923 *Radulopecten vagans* (J. de C. Sowerby); Lissajous, p. 160.
1923 *Radulopecten semicostatus* (Cossmann); Lissajous, p. 160.
1923 *Radulopecten Romani* sp. nov; Lissajous, p. 162, pl. 30, figs. 4, 4a, 4b, 5, 5a, 5b.
1926 *Aequipecten vagans* (J. de C. Sowerby); Staesche, p. 67.
1926 *Chlamys vagans* (J. de C. Sowerby); Roman, p. 178.
1929 *Pecten (Chlamys) vagans* J. de C. Sowerby; Lanquine, p. 323.
1932 *Chlamys vagans* (J. de C. Sowerby); Douglas and Arkell, pp. 130, 131, 158.
v 1932 *Chlamys* cf. *anisopleurus* (Buvignier); Douglas and Arkell, pp. 130, 140.
v 1936 *Aequipecten vagans* (J. de C. Sowerby); Dechaseaux, p. 43, pl. 6, figs. 1, 2, 3, 9.
v 1936 *Aequipecten vagans* var. *anomalus* (Terquem and Jourdy); Dechaseaux, p. 44, pl. 6, figs. 5, 7, 8, 14.
1936 *Aequipecten vagans* var. *hemicostatus* (Morris and Lycett); Dechaseaux, p. 45.
v 1936 *Aequipecten Rushdenensis* (Lycett); Dechaseaux, p. 46, pl. 6, figs. 10, 11.
v 1936 *Aequipecten* cf. *Romani* (Lissajous); Dechaseaux, p. 47, pl. 6, fig. 12.
1936 *Aequipecten anisopleurus* (Buvignier); Dechaseaux, p. 49.
1940 *Chlamys vagans* (J. de C. Sowerby); Parent, p. 42.
1948 *Chlamys (Radulopecten) hemicostata* (Morris and Lycett; Cox and Arkell, p. 12.
1948 *Chlamys (Radulopecten) vagans* (J. de C. Sowerby); Cox and Arkell, p. 12.
1948 *Chlamys (Radulopecten) anisopleurus* (Buvignier); Cox and Arkell, p. 12.
1948 *Chlamys (Radulopecten) wollastonensis* (Lycett); Cox and Arkell, p. 13.
1948 *Chlamys (Radulopecten) griesbachi* (Lycett); Cox and Arkell, p. 13.
1948 *Chlamys (Radulopecten) rushdenensis* (Lycett); Cox and Arkell, p. 13.
1950 *Chlamys (Radulopecten) vagans* (J. de C. Sowerby); Channon, p. 246.
1961 *Chlamys vagans* (J. de C. Sowerby); Barbulescu, p. 701.
1964 *Chlamys (Radulopecten) hemicostata* (Morris and Lycett); J.-C. Fischer, p. 17.
1971 *Radulopecten vagans* (J. de C. Sowerby; Mauberge, pp. 25–28.
1971 *Radulopecten vagans* var. *anomalus* (Terquem and Jourdy); Mauberge, pp. 25–28, 3 text figs.

Lectotype of *Pecten vagans* J. de C. Sowerby 1826a, p. 82, pl. 543, figs. 3, 4, 5 designated Arkell, 1931b, p. 437; BM 43319 (the original to J. de C. Sowerby's pl. 543, figs. 3, 4); Pl. 9, Fig. 31 herein; H: 41, L: 35; L. Cornbrash (Bathonian) fide Arkell (1931b), Chatley, Somerset. Paralectotype; also BM 43319 (the original to J. de C. Sowerby's pl. 543, fig. 5); Bradford Clay or Fuller's Earth (Bathonian) fide Arkell (1931b), Loscombe, Somerset.

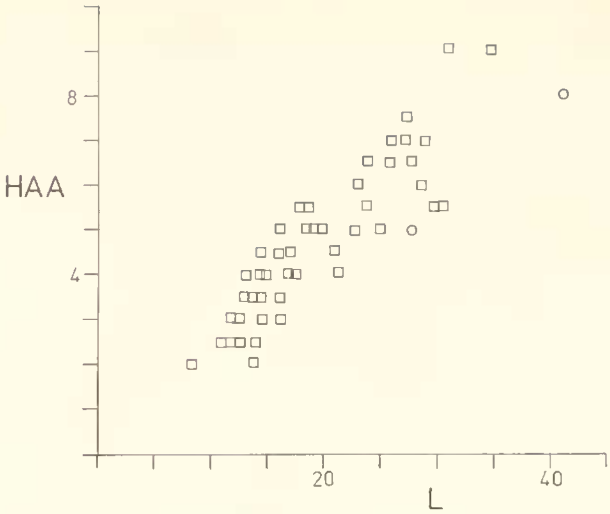


Text fig. 168: *Radulopecten vagans* – height/length.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

'Rather convex, a little longer than wide; ribs 11, large, convex, decorated with large erect concave scales that are very close upon the right but distant upon the left valve; ears nearly equal, crossed by large scales.

Syn. *P. sulcatus*. Geol. Survey of the Yorkshire Coast, p. 233, t. 9, fig. 3. excl. Syn.



Text fig. 169: *Radulopecten vagans* – height of anterior auricle/length.

Seldom above an inch and a quarter wide. It differs from the last [‘*Pecten*’ *vimineus*] by having only half the number of ribs, and in not having the regular concentric striae which appear between the ribs in that. When young the ribs are but a little raised, although the scales are then large: a few obscure rays sometimes appear between the ribs.

This is one of those few shells which appear in several strata: it is found in clay belonging to the oolite near Bath (fig. 5); in the Bath or Great Oolite at Hampton, Gloucestershire, and Bradford, Wiltshire; above the Oolite at Ancliffe, in the Cornbrash at Chatley (figs. 3 and 4), and in the Oolite Limestone at Malton.’

2. AMENDED DIAGNOSIS

Distinguished from *R. varians* by the smaller number of initial plicae, from *R. strictus* by the smaller number of radial striae, from *R. inequicostatus* by the relatively uniform size of the initial plicae and from all other species of *Radulopecten* by the existence of a non plicate phase early in ontogeny.

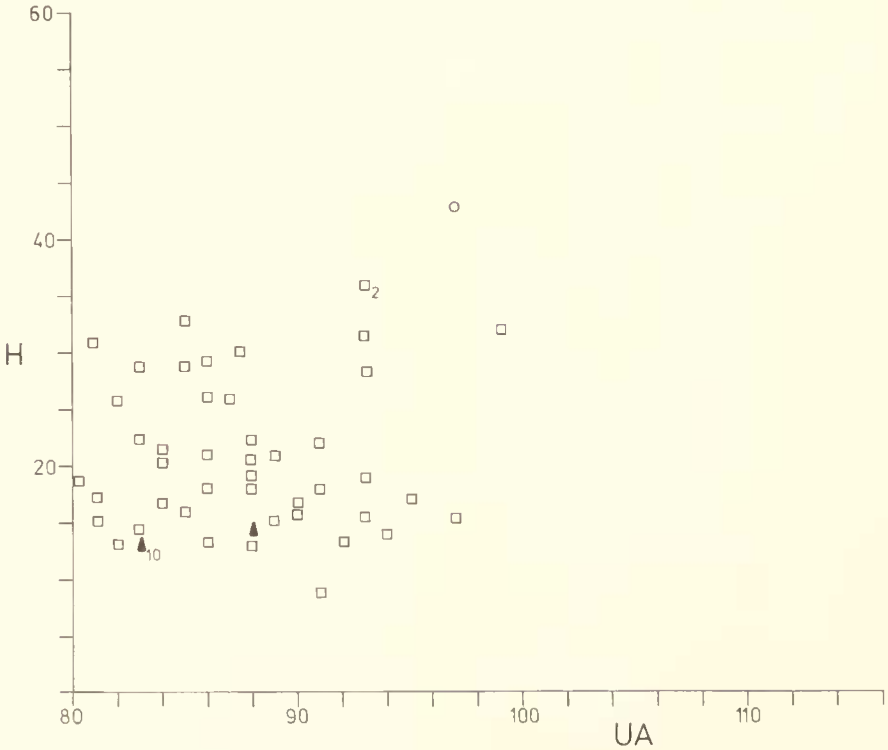
3. AMENDED DESCRIPTION

Disc sub-ovate, higher than long, increasing in size isometrically (text fig. 168) to a known maximum height of 50 mm (OUM J4821, BM L91533) but possibly reaching heights as great as 80 mm (see Section 7). Umbonal angle variable (text fig. 170), increasing only slightly during ontogeny. Disc flanks moderately high.

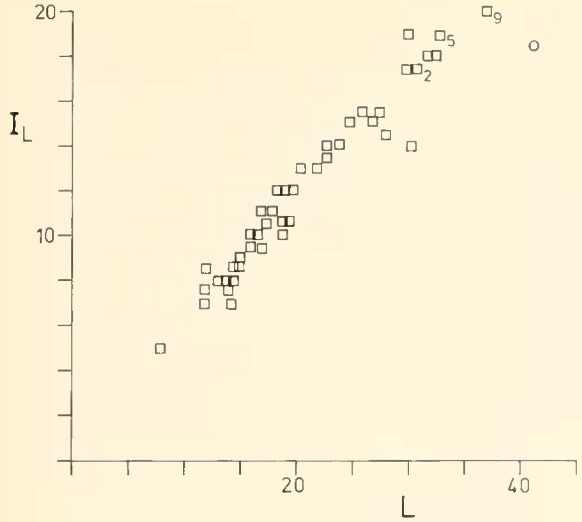
Equilateral, usually inequivalve with left valve more convex than right but all variations between latter and forms with right valve more convex than left. Convexity low – moderate in both valves. Intersinal distance greater in left valve than right, increasing with approximate isometry in both (text figs. 171, 172). Byssal notch depth variable, usually moderate (text fig. 173), increasing with approximate isometry.

Auricles well demarcated from disc; size variable (e. g. Pl. 9, Figs. 19, 33) usually moderate, anterior slightly larger than posterior. Posterior auricles usually meeting hinge line at 90°; anterior auricles meeting hinge line at 90° or less. Anterior auricle of right valve meeting disc at an obtuse angle; remaining auricles meeting disc at an acute angle. All auricles ornamented with comarginal lamellae.

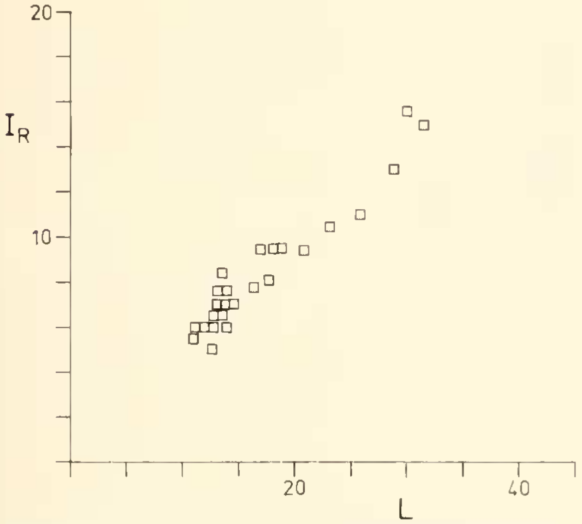
Height of anterior auricle (text fig. 169) and lengths of anterior (text fig. 174) and posterior (text fig. 175) hinges variable but increasing with approximate isometry.



Text fig. 170: *Radulopecten vagans* – height/umbonal angle.



Text fig. 171: *Radulopecten vagans* – intersinal distance on left valve/length.



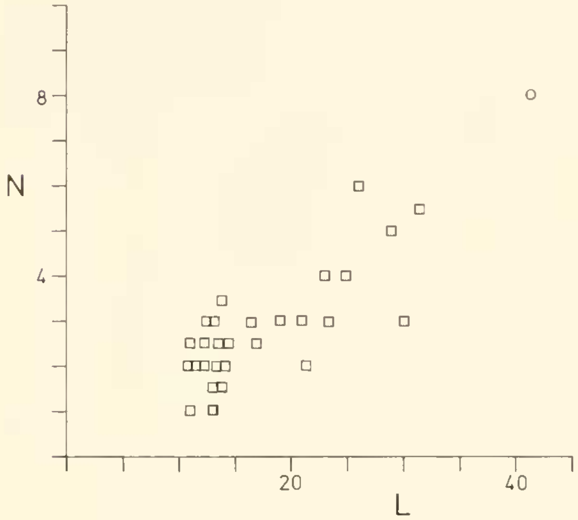
Text fig. 172: *Radulopecten vagans* – intersinal distance on right valve/length.

Ornament of right valve variable (e. g. Pl. 9, Figs. 23–25, 30). Between 4 and 14 low plicae, wider than sulci and increasing in number by splitting. Usually less than 4% but sometimes the major proportion of specimens from a given locality also bearing up to 50 (usually about 30) radial striae (see Section 4). All specimens bearing closely spaced comarginal striae, sometimes interrupted to form a decussate pattern. In late ontogeny of specimens with relatively high plicae, comarginal striae absent from sulci and raised into lamellae on plicae.

Ornament of left valve extremely variable (e. g. Pl. 9, Figs. 9–22, 26–29, 31–33), essentially consisting of 2 zones. Earlier ontogenetic stages exhibiting between 15 and 35 (MNO 2901 B), most commonly about 25, radial striae crossed by comarginal striae which are sometimes interrupted to form a decussate pattern. Later ontogenetic stages characterised by the development of between 4 and 14 (MNP), most commonly 5, radial striae into low plicae which are narrower than the sulci and bear variably spaced comarginal lamellae. Remaining radial striae rarely persisting and comarginal striae becoming decussate or absent in the sulci. Further plicae added by intercalation to a maximum number of 16 (BM 65889), most commonly 9. Height of non-plicate zone extremely variable; from a few to 37 mm (BM L76308). Number of plicae at a given height extremely variable; 0–11 (GPIG) at H: 10, 0–14 (MNP) at H: 15, 0–14 (MNP) at H: 20, 5 (BM 66243) – 14 (MNP) at H: 25, 6 (MNP) – 15 (BM 65889) at H: 30, 7 (MNO) – 16 (BM 65889) at H: 35. Geographically and stratigraphically separated samples tending, however, to have a characteristic mean and coefficient of variation for the number of plicae at each height (see Johnson, 1981).

Shell thickness moderate.

The author has presented elsewhere (Johnson, 1981) his reasons for considering the large range of variation described above to be the product of developmental flexibility within a single species.



Text fig. 173: *Radulopecten vagans* – depth of byssal notch/length.

4. DISCUSSION

As the earliest taxonomic species with type specimens within the range of the species described in Section 3 '*Pecten*' *vagans* J. de C. Sowerby is the senior synonym for the latter. The lectotype (BM 43319; Pl. 9, Fig. 31; 1) is a form in which plicae were introduced very early in ontogeny ('early developer') and has 11 plicae at H: 41. J. de C. Sowerby indicates by synonymising '*P.*' *sulcatus* Young and Bird with '*P.*' *vagans* that he included forms which the present author places in *Radulopecten fibrosus* within his hypodigm for '*P.*' *vagans*. Such forms are probably the basis for his record of '*P.*' *vagans* from the Oxfordian (Malton Oolite), a horizon at which *R. fibrosus* is abundant but *R. vagans* (i. e. the species described in Section 3) is either extremely rare or absent (see Section 5). A similar inclusion of forms which are referable to *R. fibrosus* may account for Roemer's (1839) and Dechaseaux's (1936) records of J. de C. Sowerby's species from the Oxfordian.

Specimens referred to '*P.*' *vagans* by Damon (1860, 1880) and Borissiak and Ivanoff (1917) are definitely referable to *R. fibrosus*.

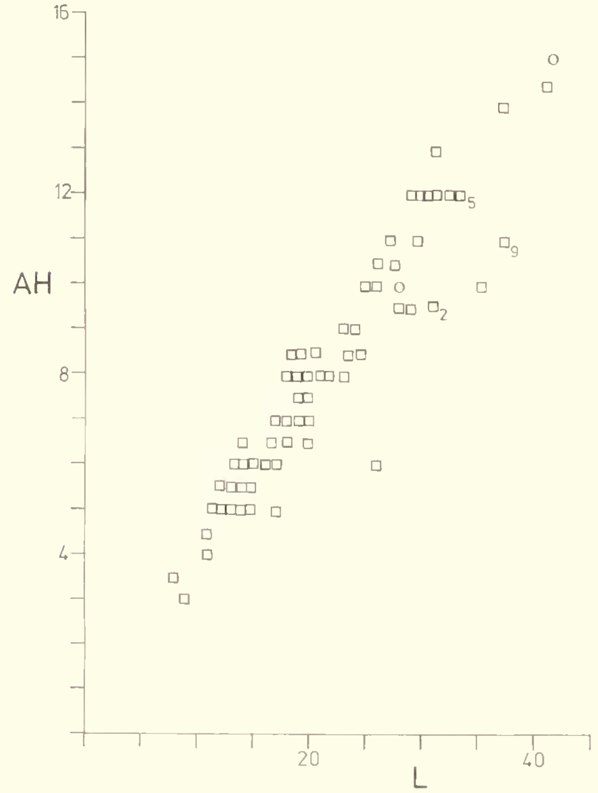
Goldfuss (1833) has applied J. de C. Sowerby's specific name to specimens said by Schlosser (1911) to be broken examples of *Ctenostreon*.

One of the syntypes of *'Lima' Nerina* d'Orbigny (MNO 2879) is indeed a nember of the Limidae but the other two (MNO 2879A; Pl. 9, Figs. 15, 22; 2) are 'intermediate developers' of *R. vagans* with 10 plicae at H: 36 and 6 plicae at H: 23 respectively. The single measurable syntype of *'P.' Rhetus* (MNO 2902; 3) is similarly an 'intermediate developer' and has 6 plicae at H: 21.5. Boule (1912) erroneously described and figured the two syntypes of *'L.' Nerina* which belong in *R. vagans* under *'P.' Rhetus*. Cossmann (1906) thought that forms like *'P.' Rhetus*. (sensu d'Orbigny) were specifically distinct but that d'Orbigny's description did not constitute an adequate indication. He therefore erected the more fully characterised *'Chlamys' semicostata* as a replacement specific name.

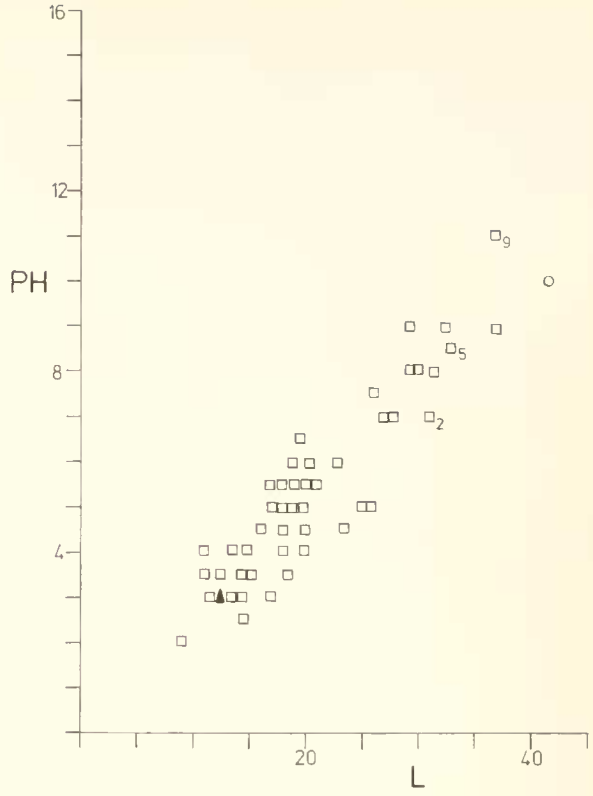
The original figure of *'P.' anisopleurus* Buvignier (4) depicts a 'late developer' with 5 plicae at H: 28.

The lectotype of *'P.' peregrinus* Morris and Lycett (IGS 9170; 5) is a large 'early developer' (with 9 plicae at H: 10, 11 at H: 15 and 13 at H: 20–35) while the lectotype of *'P.' hemicostatus* Morris and Lycett (IGS 9168; Pl. 9, Fig. 18; 6) is a small 'intermediate developer'.

The sole observed type of *'P.' Wollastonensis* Lycett (BM L76311; Pl. 9, Fig. 9; 7) and the syntypes of *'P.' Rushdenensis* Lycett (BM L76309, L76310; Pl. 9, Fig. 16; 8) are all clearly 'late-developing' forms of *R. vagans*, *'P.' Wollastonensis* exhibiting the typical continuous comarginal striae and *'P.' Rushdenensis* the more unusual decussate pattern. The sole observed type of *'P.' Griesbachi* Lycett (BM L76308; 9) is only distinguishable from the 'late developer' phenotype of *R. vagans* by a lack of striae and this can almost certainly be accounted for by abrasion.



Text fig. 174: *Radulopecten vagans* – anterior hinge length/length.



Text fig. 175: *Radulopecten vagans* – posterior hinge length/length.

The holotype (M) of *'P.' intermittens* Whidborne (SM J4759; 10) is a small 'late developer' with 19 radial striae.

The left valve figured under *'P.' anomalus* Terquem and Jourdy has 14 plicae and is indistinguishable from *R. vagans*. However, the right valves have about 30 radial striae and are thus quite unlike typical right valves of *R. vagans*. Similar forms (e. g. Pl. 9, Fig. 25) occur widely in the M. Jurassic and since there appear to be no intermediate right valve morphologies it may be that they should be accorded a specific distinction from *R. vagans* under Terquem and Jourdy's name. However, the present author is aware of no locality at which 'striate' morphs occur in the absence of 'non-striate' morphs. It therefore seems more likely that they are polymorphs of the same species rather than representatives of different species. Mauberge (1971) has gone so far as to suggest that they may be sexual dimorphs but the stratigraphic change in relative abundance of the morphs (see Sections 7, 10) seems to argue against this particular hypothesis.

Inclusion of the 'striate' morph within *R. vagans* means that *R. Romani* Lissajous and *'Ch.' rosimon* Cossmann (non d'Orbigny), both of which were based on such specimens, must be synonymised with *R. vagans*.

The original figure of *'P.' Thurmanni* Contejean (11) appears to depict an early developing form of *R. vagans* with 9 or 10 plicae at H: 10. However, the stratigraphic horizon (Kimmeridgian) is anomalously late for the latter species (see Section 5) and suggests that the figure may be a poor representation of an example of *R. varians*. Dechaseaux (1936) considers Contejean's species to be closer to *R. fibrosus*.

De Gregorio's figure of *'P.' samilus* shows no more than a poorly preserved internal mould while that of *'P.' eglus* is only 5 mm high. However, both species exhibit 9 plicae and have a general form which suggests that they may be synonymous with *R. vagans*.

The figured specimen of *'P.' fibrosus* J. SOWERBY; QUENSTEDT has 9 plicae, unlike J. SOWERBY's species. Since it is described as an example of a variable species from the Bathonian there can be little doubt of its identity with *R. vagans*. E. PHILLIPI's (1900) *'Aequipecten' fibrosus* is similarly referable to J. DE C. SOWERBY's species.

ARKELL (1931a) examined the original (SM) to LYCETT's illustration (1863, pl. 33, fig. 1a) of *'P.' inaequicostatus* PHILLIPS and pronounced it to be a representative of *'Ch.' (R.) anisopleurus* (BUVIGNIER), a species considered above to be a junior synonym of *R. vagans*.

5. STRATIGRAPHIC RANGE

Excluding GOLDFUSS' (1833) invalid record of the species from the German Lias (see Section 4) the earliest certain record of *R. vagans* is provided by a single specimen (BM L17615) from the Murchisonae zone (Aalenian) of the Cotswolds. Two specimens of questionable affinities (see Section 4) from strata in the Bifrons-Murchisonae zones of Sicily (DE GREGORIO, 1886a, c) may be derived from a lower horizon. Only one other specimen (NM) is known from the Aalenian.

In the L. Bajocian specimens are known from the L. Trigonia Grit of the Cotswolds (BM L95380) and the Scarborough Limestone of Yorkshire (YM 500).

In the U. Bajocian, *R. vagans* becomes quite common but it seems likely that the increase in numbers did not occur until the latest parts of the substage since all records which can be assigned to a zone (LISSAJOUS, 1910; PARIS and RICHARDSON, 1916; CHANNON, 1950; sundry specimens in the BM, OUM, and GPIT) are derived from the Parkinsoni zone.

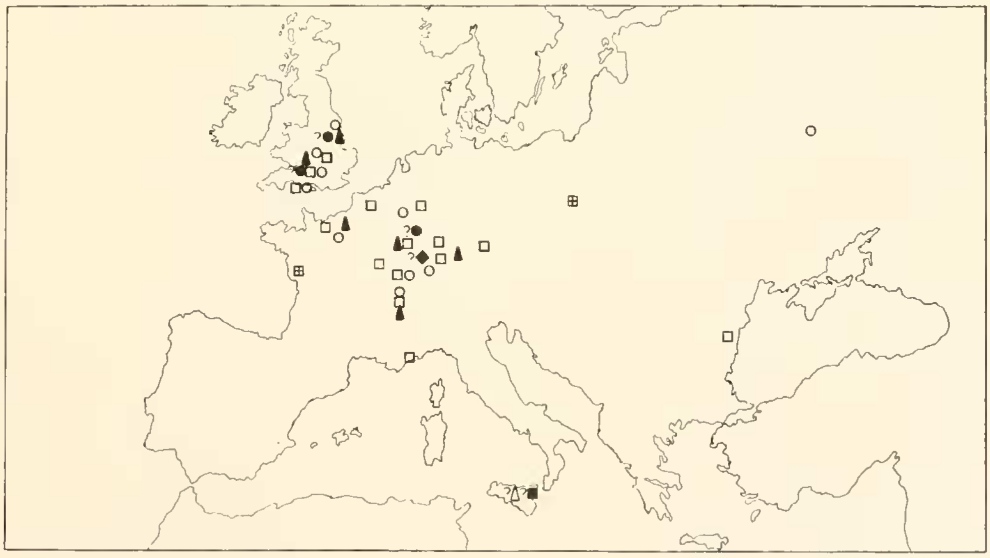
The species is found at almost all horizons in the Bathonian, locally becoming extremely abundant.

In the Callovian *R. vagans* is reported to be common in the U. Cornbrash (Macrocephalus zone) of England by COX and ARKELL (1948). However, this is not borne out by the author's field work in Yorkshire and only 10 museum specimens (BM L91533, L91559, L91580; OUM J4821, J4822, J37587; SbM; DM[3]) are known from this and equivalent horizons in Europe. The only other Callovian museum specimens assignable to a zone are 3 (BM 47436, L17969[2]) from the Kellaways Rock (Calloviense zone) of Yorkshire. ROLLIER (1911) records *R. vagans* from the L.-M. Callovian of the Jura and BORISSIAK and IVANOFF (1917) record the species from the M. Callovian of Russia. Other bibliographic records from the Callovian (BUVIGNIER, 1852; DECHASEAUX, 1936), apart from those referring to the Macrocephalus zone (e. g. BEAN, 1839; LISSAJOUS, 1910; DOUGLAS and ARKELL, 1932), cannot be assigned to a substage. *R. vagans* is not known to be common anywhere in the Callovian.

Two specimens from the Oxfordian (probably Plicatilis zone) of Berkshire (BM 9930) and Yorkshire (BM L3634; Pl. 9, Fig. 34) appear to be representatives of *R. vagans* but the possibility cannot be entirely excluded that they are extreme variants of *R. inequicostatus*. Oxfordian specimens mentioned in J. DE C. SOWERBY (1826), ROEMER (1839) and DECHASEAUX (1936) and Kimmeridgian specimens mentioned in CONTEJEAN (1859) may also be representatives of *R. vagans* (see Section 4).

6. GEOGRAPHIC RANGE

R. vagans is generally rare in the peri-Mediterranean region (text fig. 176) and is unknown outside Europe. In the Bathonian the paucity of locally derived specimens in museums at Dijon, Tübingen and Munich compared with the abundance of specimens known from N. France and S. England suggests a latitudinal temperature control on distribution. However, bibliographic records of the species further south, although sparse, occasionally refer to numerous specimens (e. g. LISSAJOUS, 1923; LANQUINE, 1929). It therefore seems more likely that the distribution of the species is a function of facies rather than temperature and that the increase in abundance from E. France/S. Germany to N. France/S. England is a reflection of a higher frequency of the appropriate facies (see Section 8).



Text fig. 176: *Radulopecten vagans* – European distribution.

7. DESCRIPTION OF ECOLOGY

The first time that *R. vagans* occurs in any numbers is in the Parkinsoni zone when it is found in S. W. Germany and the Cotswolds. In the latter area the sediments (Clypeus Grit) are bioturbated, oolitic limestones in which the 'striate' morph seems to be dominant (see Section 10), reaching a maximum height of 27 mm (OUM J36384). The largest Bajocian specimen (H: 35; BM L95380) is from the L. Trigonia Grit (L. Bajocian).

R. vagans becomes locally abundant in the Bathonian and the following account concentrates on such occurrences.

In the L. Bathonian (Progracilis zone) the species occurs in grain-supported shelly oolitic limestones at Minchinhampton and Taynton in the Cotswolds. There is an abundant and diverse fauna of bivalves and gastropods but ammonites are rare. At the former locality fairly large 'early developers' are relatively common but no representatives of the 'striate' morph have been noted. Although most specimens are disarticulated the incidence of abrasion and breakage is low enough to suggest minimal transport.

In the M. Bathonian (Subcontractus zone) of Lorraine the species occurs in the Caillasse à *Anabacia (= Chomatoseris)*. Estimates of the relative abundance of the 'striate' morph in this area range from 1% (Mauberge, 1971) to about 50% (Dechaseaux, 1936). G. A. Gill (pers. comm., 1977) reports that *R. vagans* is a frequent associate of *Chomatoseris* (Zoantharia) in poorly sorted oolites and biosparites at other localities in France.

In the U. Bathonian small 'early developers' are the dominant forms of *R. vagans* present in the lower part of the Boueti Bed (Aspidoides zone) at Herbury (Dorset). 'Striate' morphs are unknown. The sediments are calcareous marls with an extremely abundant but low diversity fauna dominated by the bivalves *Acromytilus* and *'Liostrea'*, the brachiopods *Digonella* and *Goniorhynchia* and ectoprocts. Most specimens of *R. vagans* are disarticulated but the low incidence of abrasion and breakage indicates minimal transport. Specimens in the upper part of the Boueti Bed and at an equivalent horizon at Amfreville (Normandy) are also heavily encrusted with the ectroproct *Attractoecia*. At the same level at Ranville large bivalved 'late developers' occur in a bed which earlier collectors called the 'Calcaire à Polypiers'. Similar forms occur in the slightly later Lion Caillasse (Discus zone, Hollandi subzone) at Luc, in association with rare representatives of the 'striate' morph. The sediments, overlying a hardground, are very similar to the Boueti Bed but the fauna is considerably more diverse, with at least 65 species, including ectoprocts and sponges not seen in England (T. Palmer, 1974). Ammonites are, however, unknown. *R. vagans* also occurs in clays above a hardground at the same horizon in Wiltshire (Bradford Clay) and in the same region occurs in clays of the slightly later Discus subzone. Specimens from the latter horizon are usually fairly large, bivalved 'early developers' and the 'striate' morph is unknown. Serpulid encrustation is heavy but almost invariably restricted to the left valve. Specimens from the same level in Oxfordshire are mainly small 'early developers' but two 'striate' morphs (out of a total of 55 right valves collected by the author from Shipton Cement Works) are known. Almost all specimens are univalved but abrasion and breakage are limited enough to suggest minimal transport. The sediments are non-oolitic, shell-fragment limestones containing an abundant and diverse in- and epibenthos (see p. 128) but few ammonites.

Apart from the Mâconnais (Lissajous, 1923) and Provence (Lanquine, 1929) where the stage is developed in shallow water marls and limestones, *R. vagans* is not known to be common elsewhere in the Bathonian, although records are widespread (text fig. 176). Prior to the Discus subzone the species is absent north of a line running west/east just south of Banbury and Brackley in England (Bradshaw, 1978). The maximum height attained in the Bathonian is 44 mm (MNO 2901; Discus zone; 'late developer').

Specimens from the calcarenites of the U. Cornbrash (Macrocephalus zone; L. Callovian) of England (see Section 5) are mainly large 'late developers'. The maximum height is 51 mm (OUM J4821, BM L91533). Borissiak and Ivanoff's (1917) figures of specimens from the M. Callovian of central Russia have a maximum height of 80 mm and there is no suggestion of photographic enlargement.

8. INTERPRETATION OF ECOLOGY

The absence of *R. vagans* from pelagic limestones in the peri-Mediterranean region suggests an intolerance of soupy substrates. However, co-occurrence with *Chomatoseris*, an auto-mobile solitary coral which is highly characteristic of loose, soft sands (Gill and Coates, 1977), indicates a tolerance of coarse grained unstable substrates. Tolerance of laterally shifting sediments is indicated by the occurrence of the species in oolites (e. g. Minchinhampton) while a more general tolerance of instability in the physical environment is indicated by the widespread occurrence of *R. vagans* in deposits where ammonites are lacking and more localised occurrence in deposits (e. g. Boueti Bed) where even the bivalve fauna is reduced in diversity. However, eurytopy was insufficiently developed to allow colonisation of the highly unstable marginal marine environments which were present in central England during much of the Bathonian (Bradshaw, 1978).

By far the most common occurrence of *R. vagans* is immediately above hardgrounds or in minimally transported or in situ shell beds with an abundance of other shelly epibenthos (e. g. Luc, Amfreville, Herbury, Bradford-on-Avon). This suggests that the existence of hard substrates was the major factor controlling distribution (see Section 9) and implies that the abundance of the species at Minchinhampton is more a reflection of the abundance of shelly epibenthos than of a particular liking for shifting substrates. The abundance of the species at Shipton may likewise be a consequence of the unusual richness of the associated epibenthos.

Since serpulid worm encrustation of bivalved specimens is limited to the left valve it seems likely that the right valve was tightly adpressed against the substrate during life (see Section 9). Ectoproct encrustation probably occurred after death since bivalved specimens are rarely encrusted.

There is a strong suggestion of a competitive reaction between *R. vagans* and *Chlamys (Ch.) textoria*. The latter, a species exhibiting considerable substrate eurytopy in the Bajocian, is largely confined to organic build-ups during the

Bathonian (the acme of *R. vagans*) and the author knows of no locality at which both species have been found in numbers.

The author has presented elsewhere (Johnson, 1981) an analysis which suggests that in much the same way as in the Recent species *Chlamys dieffenbachi* (see Beu, 1966), plical variation in *R. vagans* reflects ecophenotypic reaction to environmental differences which were developed over the space of a few metres. In the case of *Ch. dieffenbachi* environmental heterogeneity is due to the patchy distribution of sponge substrates. Since the associated sediments have not been closely examined for the presence of spicules, it cannot be ruled out that *R. vagans* also developed different patterns of plication according to whether or not sponges constituted the substrate for attachment. That other soft-bodied organisms were involved is, of course, also a possibility.

9. FUNCTIONAL MORPHOLOGY

The usually moderately deep byssal notch combined with small or moderate adult size (with the probable exception of a few specimens from the M. Callovian of Russia [see Section 7]) suggests that *R. vagans* was byssally attached throughout life. The generally lower convexity of the right valve and its subdued ornamentation are paradigmatic for tight fixation and variations in convexity perhaps suggest that *R. vagans* was adpressed against hard surfaces of variable shape (cf. below).

Although intercalation of new plicae would have probably led to increased shell strength and stiffness it is very doubtful whether the addition of numerous plicae in some specimens of *R. vagans* was a response to a need for a mechanically superior shell. In *Ch. dieffenbachi* a need for an increase in the density of plical spinelets in order to grip a sponge substrate seems to be the underlying reason for the adoption of a densely plicate form (Beu, 1966). A similar type of explanation involving some soft-bodied organism, even if not sponges, is suggested in *R. vagans* by the fact that the comarginal lamellae become progressively more localised onto the crests of the plicae, thereby retaining the possibility of close contact with the substrate, in the ontogenetic passage from a weakly to a strongly plicate form. If this explanation is correct then the distribution of the soft-bodied host must have been determined by the existence of hard substrates so as to produce the observed correlation between such substrates and the occurrence of *R. vagans*.

The presence of upstanding ornament and absence of anything more than minimal ontogenetic increase in umbonal angle must have greatly restricted swimming ability in *R. vagans*.

10. ORIGINS AND EVOLUTION

The origins of *R. vagans* are a mystery. The author is aware of no Jurassic pectinid species which can be regarded as a likely forebear. The ancestry of *R. vagans* may be connected with the largely Asiatic Triassic genus *Indopecten*.

R. vagans exhibits phyletic evolution in right valve morph frequency. Samples from the Bajocian only include a small proportion of the 'non-striate' morph but by the L. Bathonian (Progracilis zone) this morph was dominant, perhaps as the result of some selective superiority. There also seems to be an evolutionary change in maximum height from the Bathonian to the Callovian. Forms possessing a similar 'late developer' phenotype (which thus rules out any chance of a purely ecophenotypic difference) reach a maximum height of 44 mm in the former stage and 51 mm in the latter stage.

The Callovian decline of *R. vagans* was probably the result of the widespread development of argillaceous facies producing soft sediments unfavourable for colonisation by the host organism (see Section 9).

Radulopecten varians (Roemer 1836)

Pl. 10, Figs. 1–3; text figs. 177–180

Synonymy

1836	*Pecten varians* sp. nov; ROEMER, p. 68, pl. 3, fig. 19.
? 1852	*Pecten Beaumontinus* sp. nov; BUVIGNIER, p. 24, pl. 19, figs. 26–30.
? 1859	*Pecten Thurmanni* sp. nov; CONTEJEAN, p. 315, pl. 23, figs. 10–12.
? 1859	*Hinnites clypeatus* sp. nov; CONTEJEAN, p. 317, pl. 24, fig. 14.
1860	*Pecten varians* ROEMER; COQUAND, p. 79.
? 1862	*Pecten Banneanus* sp. nov; ÉTALLON in THURMANN and ÉTALLON, p. 259, pl. 36, fig. 12.
? 1862	*Pecten Pagnardi* sp. nov; ÉTALLON in THURMANN and ÉTALLON, p. 259, pl. 36, fig. 12.
1862	*Pecten qualicosta* ÉTALLON in THURMANN and ÉTALLON, p. 260, pl. 36, fig. 13.
non 1862	*Pecten beaumontinus* BUVIGNIER; THURMANN and ÉTALLON, p. 260, pl. 36, fig. 14.
1863	*Pecten perstrictus* sp. nov; ÉTALLON, p. 56, pl. 8, fig. 8.
1864	*Pecten varians* ROEMER; V. SEEBACH, p. 98.
1871	*Pecten Urius* sp. nov; SAUVAGE and RIGAUX, p. 354.
1872	*Pecten Urius* SAUVAGE and RIGAUX; SAUVAGE and RIGAUX, p. 176, pl. 9, fig. 5.
1875	*Pecten qualicosta* ÉTALLON; DE LORIOL and PELLAT, p. 202, pl. 22, figs. 18–20.
1893	*Pecten beaumontinus* BUVIGNIER; DE LORIOL, p. 305, pl. 32, fig. 18.
1893	*Pecten qualicosta* ÉTALLON; DE LORIOL, p. 306, pl. 32, fig. 20.
1900	*Pecten varians* ROEMER; E. PHILIPPI, p. 99, text fig. 16a.
v 1905	*Pecten qualicosta* ÉTALLON; PERON, p. 221.
v 1905	*Pecten beaumontinus* BUVIGNIER; PERON, p. 230.
1917	*Pecten* cf. *qualicosta* ÉTALLON; BORISSIAK and IVANOFF, p. 49, pl. 3, fig. 2.
1917	*Pecten donezianus* sp. nov; BORISSIAK and IVANOFF, p. 52, pl. 3, figs. 5–12.
? 1921	*Chlamys Beaumontina* (BUVIGNIER); COSSMANN, p. 6, pl. 1, fig. 1.
1926	*Chlamys (Aequipecten) qualicosta* (ÉTALLON); ARKELL, p. 548, pl. 32, figs. 4, 5.
pv 1931a	*Chlamys (Chlamys) qualicosta* (ÉTALLON); ARKELL, p. 111, pl. 11, figs. 2–5.
1936	*Aequipecten qualicosta* (ÉTALLON); DECHASEAUX, p. 51, pl. 7, figs. 7–21.
v 1936	*Aequipecten Beaumontinus* (BUVIGNIER); DECHASEAUX, p. 53, pl. 8, fig. 4.
1936	*Aequipecten perstrictus* (ÉTALLON); DECHASEAUX, p. 56, pl. 8, fig. 8.
v* 1936	*Aequipecten Buvignieri* sp. nov; DECHASEAUX, p. 58, pl. 8, fig. 2.

? 1952 *Chlamys (Radulopecten) qualicosta* (ÉTALLON); CHAVAN, p. 37, pl. 2, fig. 15.

The type material of *Pecten varians* ROEMER 1836, p. 68, pl. 3, fig. 19 is probably in the ROEMER-PELIZAEUS-Museum, Hildesheim, W. Germany. The material was derived from the Oxfordian of N. Germany.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

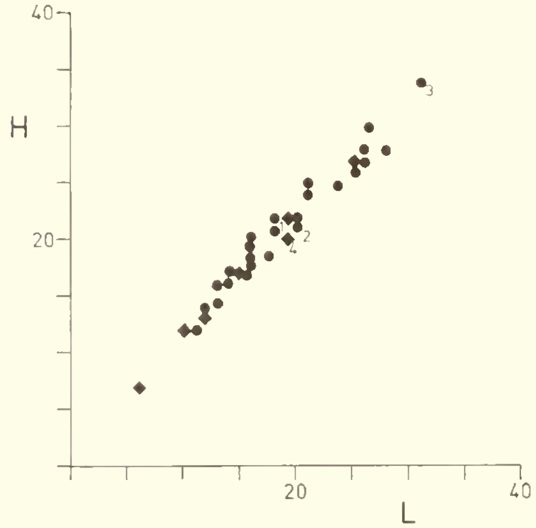
'*P.* testa ovato-orbiculari convexo plana radiatim striata, valva sinistra convexiore, striis subinaequalibus lineis concentricis in striarum longitudinalium dorso lamelloso squamosis decussatis, auriculis inaequalibus longitudinaliter striatis.

Das Gehäuse ist eirund, oder fast kreisrund; die Schalen sind beide gewölbt, die linke am meisten; beide sind mit zahlreichen ungleichen Längsstreifen besetzt, auf denen die concentrischen Linien blättrige Schuppen bilden; diese sind gewöhnlich nur am unteren Teile der Schalen deutlich, fehlen aber selten ganz. Die Ohren sind ungleich längsgestreift und wenig quer-liniert.

Ist gewöhnlich etwas kleiner als das abgebildete Exemplar und findet sich im oberen Coral Rag bei Hoheneggelsen so wie am Galzenberge bei Hildesheim.'

2. AMENDED DIAGNOSIS

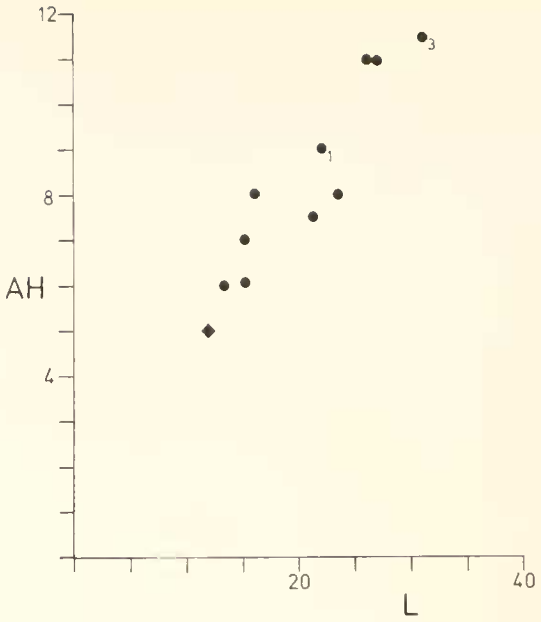
Differing from *R. vagans*, *R. strictus* and *R. inequicostatus* by the larger number of initial plicae and from all other species of *Radulopecten* by the existence of a non-plicate phase early in ontogeny.



Text fig. 177: *Radulopecten varians* – height/length.

3. AMENDED DESCRIPTION

Disc sub-ovate, higher than long, early in ontogeny growing allometrically (text fig. 177) to become sub-orbicular near the maximum height of 33 mm (NM). Umbonal angle variable (text fig. 179), increasing slightly during ontogeny to produce concave dorsal margins. Disc flanks low.



Text fig. 178: *Radulopecten varians* – anterior hinge length/length.

Equilateral; inequivalve, left valve more convex than right, both low convexity. Intersinal distance greater in left valve than right; moderate sized byssal notch.

Auricles well separated from disc, moderate in size, anterior slightly larger than posterior. Anterior auricles meeting hinge line and disc at a right angle; posterior auricles meeting hinge line at a right or obtuse angle and disc at an acute angle. Anterior auricles ornamented with 2–4 radial costae. Anterior hinge length moderate (text fig. 178).

Right valve ornamented near the umbo with closely spaced comarginal striae and usually a large number of very fine radial striae. Latter developing into plicae at shell heights above about 10 mm to match those on the left valve (Pl. 10, Fig. 1). Comarginal ornament tending to become reduced in the sulci.

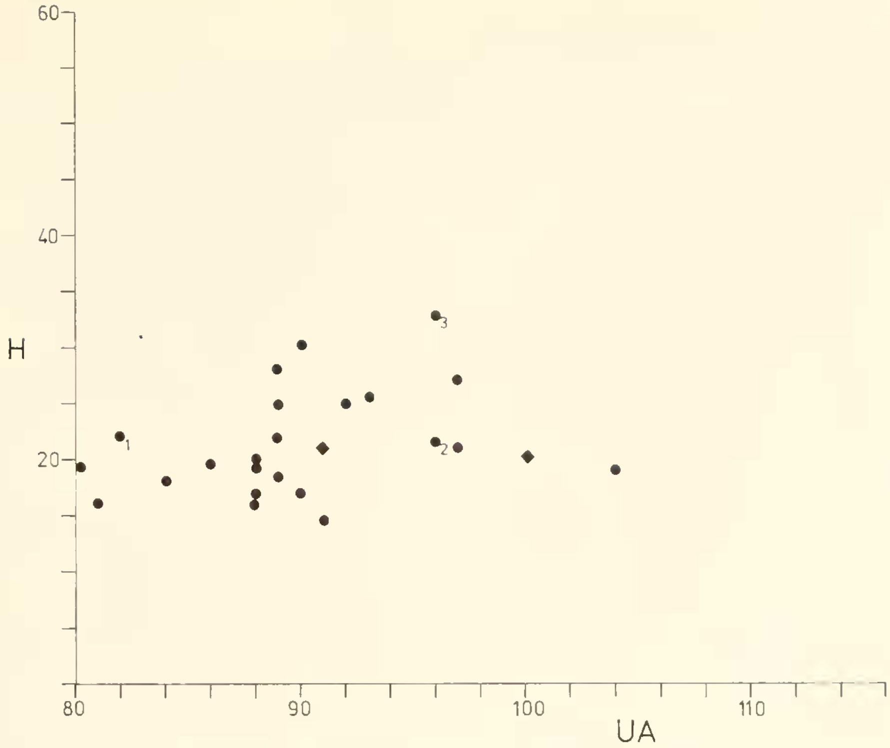
Left valve also ornamented with comarginal striae near the umbo. All specimens possessing about 40 radial striae of which initially about 15 develop into narrow plicae to be followed, at a variable rate, by the remainder such that at H: 20 there are between 16 (OUM J1891) and 39 (OUM J9005) plicae and at H: 30 between 20 (BM 33423) and 40 (MNO 4293) plicae (Pl. 10, Figs. 2,3). Comarginal striae expanding into lamellae on the crests of the plicae and tending to disappear in the sulci.

Shell thickness moderate.

4. DISCUSSION

ROEMER's (1836) figure of '*Pecten*' *varians* depicts a right valve whose number of plicae (ca. 28 at H: 22) and metric proportions (1) fall within the range of the species described in Section 3. Since ROEMER's name is the earliest available the latter is known hereinafter as *Radulopecten varians*.

There is some doubt over the affinities of '*P.*' *Beaumontinus* BUVIGNIER. This species and subsequent references thereto is discussed under *R. strictus* (MÜNSTER). Since ÉTALLON's (1862) '*P.*' *Banneanus* was allied to BUVIGNIER's species

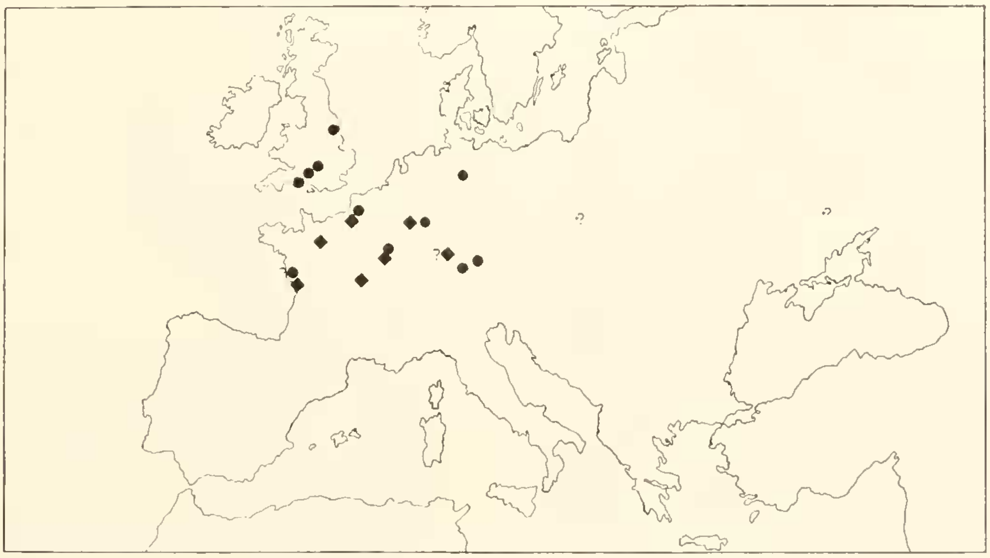


Text fig. 179: *Radulopecten varians* – height/umbonal angle.

and his '*P.*' *Pagnardi* to MÜNSTER's species some doubt must remain as to the affinities of these species in spite of the fact that the figures of both appear to depict examples of *R. varians*. The figure of '*P.*' *qualicosta* ÉTALLON undoubtedly depicts a specimen of *R. varians* as does DE LORIOL's (1893) figure of a specimen (repository: École Cantonale de Porrentruy, Switzerland) chosen as lectotype. CHAVAN's (1952) record of '*Chlamys*' *(R.) qualicosta* appears to be a misnomer for *R. fibrosus* (q. v.).

ÉTALLON's (1863) original reference to '*P.*' *perstrictus* has proved impossible to trace. However, the description has been reiterated by DECHASEAUX (1936) together with a photograph of a type, which is indistinguishable from *R. varians*. The original reference to '*P.*' *Urius* SAUVAGE and RIGAUX has similarly proved impossible to trace but the species was redescribed and figured by the same authors (1872) and the number of plicae (30 at H: 21.5) and metric proportions (2) are within the range of *R. varians*.

The holotype (M) of '*Aequipecten*' *Buvignieri* DECHASEAUX (NM) has 22 plicae at H: 33 and metric proportions (3) which are indistinguishable from those of *R. varians*. The syntype series of '*P.*' *donezianus* BORISSIAK and IVANOFF has not been studied but the photographs leave no doubt that the species should be synonymised with *R. varians*.



Text fig. 180: *Radulopecten varians* – European distribution.

The figure of *'Hinnites' clypeatus* CONTEJEAN is of a right valve unlike that of any *'Hinnites' (= Eopecten)* species but with a plical count (27 at H: 20) and metric proportions (4) which suggest that it may be a representative of *R. varians.*

The affinities of *'P.' Thurmanni* CONTEJEAN are discussed under *R. vagans.*

5. STRATIGRAPHIC RANGE

The earliest zonally defined records of *R. varians* are from the Transversarium zone (U. Oxfordian) of Dorset where the species is common. In the same area it is common in the Cautisnigrae zone (U. Oxfordian). ROEMER's (1836) specimens are probably from the Decipiens zone. It is doubtful whether 'Oxfordian' records from Switzerland (THURMANN and ÉTALLON, 1862; DE LORIOL, 1893) and France (e. g. DECHASEAUX, 1936) include any material from later horizons in the stage.

A few specimens of *R. varians* are known from the L. Kimmeridgian of east and central France (MNO 4293, MNP S04680, S04683, S05068) and one from the west coast (author's collection). The number of specimens involved in DE LORIOL and PELLAT's (1875) record from the L. Kimmeridgian of the Boulonnais is indeterminate but probably small. It is very doubtful whether DECHASEAUX's (1936) 'Kimméridgien' record includes any specimens from horizons above the lowest substage.

6. GEOGRAPHIC RANGE

Apart from isolated occurrences in the 'Jurassic' of Poland and Russia (BORISSIAK and IVANOFF, 1917), *R. varians* is entirely restricted to N. W. Europe (text fig. 180).

7. DESCRIPTION OF ECOLOGY

R. varians is first known to be common in the 'Qualicosta' Bed near the base of the Osmington Oolite Series (Transversarium zone) where it reaches a maximum height of 31 mm (author's collection). The sediments are cross-bedded but poorly sorted oobiosparites. The remaining fauna is dominated by *Nanogyra* (association G of FÜRSICH, 1977) and all the bivalves are disarticulated. *R. varians* is not common in the remainder of the series in Dorset, is rare throughout the series in N. Wiltshire, Berkshire, Oxfordshire and Cambridgeshire, where coral rag facies occur (ARKELL, 1931a), and is unknown in Lincolnshire and Norfolk where phyllosilicate clay facies are dominant (BROOKFIELD, 1973). The equivalent horizon in Yorkshire is largely developed in coral rag facies and is probably the source of the three specimens (BM 34423, L3633, L84564) which constitute the only known records of *R. varians* from the area (cf. ARKELL, 1931a).

In the *'Trigonia' clavellata* Beds of the Gloucester Oolite Series (Cautisnigrae zone) in Dorset, *R. varians* occurs commonly in the Main Shell Bed, where it reaches a maximum height of 28 mm (author's collection), and in the Red Beds. The sediments are more marly than the 'Qualicosta' Bed and have a siderite cement. The fauna is also more diverse (association D of FÜRSICH, 1977) and the bivalves, of which *Nanogyra* and *Myophorella* are the dominant genera, are occasionally articulated.

R. varians is apparently absent after the Cautisnigrae zone in Britain.

The species is not known to be common at any horizon in the Oxfordian of continental Europe, although it reaches a height of 33 mm (NM). It is known to be rare in coral reef facies in the Jura (THURMANN and ÉTALLON, 1862; DE LORIOL, 1893).

Rare specimens from the L. Kimmeridgian reach a maximum height of 27 mm (MNO 4293) and are found in association with *R. strictus.*

8. INTERPRETATION OF ECOLOGY

WILSON (1968) has interpreted the shell beds in which *R. varians* occurs commonly in Dorset as the highest parts of tidal flat regressive sequences, implying thereby that they represent strand-line accumulations of sub-littoral but nearshore organisms. However, TALBOT (1973) considered that they represented offshore environments, albeit within regressive sequences, a conclusion which is supported, at least for the *'T.' clavellata* Beds, by FÜRSICH's (1976, 1977) taphonomic analysis which indicates a stratigraphically condensed but minimally transported fauna living in a moderate energy submarine environment. Taphonomic evidence from the 'Qualicosta' Bed (see Section 7) is less indicative of an in situ fauna so WILSON's interpretation may be applicable to this horizon. The implication is therefore that distance from the shoreline played no part in determining the suitability of an area for colonisation by *R. varians.* The absence of the species from some clay (e. g. Transversarium zone in E. Anglia) and micrite (e. g. throughout the species range in many areas of S. Europe) sequences and its rarity in others indicates that low energy environments were not suitable for colonisation. The rarity of the species in reef and reef-derived sediments suggests that anything other than level bottom environments were similarly unfavourable.

The Kimmeridgian occurrences of *R. varians* imply a lack of competition with the probable descendant, *R. strictus.* There appears to be no basis for this in terms of microhabitat differences (see Section 9 and p. 202).

9. FUNCTIONAL MORPHOLOGY

Since in many morphological respects *R. varians* is identical to *R. vagans* a similar tightly byssate mode of life can be inferred. The comarginal lamellae on the left valve are, however, considerably smaller in *R. varians* so it is doubtful whether they could have served any purpose in gripping a soft substrate, as suggested for *R. vagans.* Hard substrates, such as shells, were probably used for attachment.

10. ORIGINS AND EVOLUTION

The most likely ancestor for *R. varians* is *R. vagans.* Since the first occurrence of the former species is within the geographic range of the latter it may be that speciation was sympatric. The pattern of ornament on the left valve of *R. varians* is essentially a scaled-down version of that of some 'late-developing' forms of *R. vagans.* This suggests that trans-specific evolution involved heterochronic retardation of the development of size with respect to that of 'shape'. However, since ornamental development in *R. vagans* was almost certainly under 'environmental' control trans-specific evolution must also have involved 'genetic assimilation' (Waddington, 1957). Heterochrony and 'genetic assimilation' are both probably indicative of regulatory gene volution.

There are no significant phyletic changes in *R. varians*. The disappearance of the species from England after the Cautisnigrae zone is probably the result of the widespread development of unfavourable argillaceous facies in the Decipiens zone. A similar development of argillaceous facies throughout Europe in the Kimmeridgian was almost certainly the cause of the extinction of the species early in the stage.

Radulopecten strictus (Münster, 1833)

Pl. 10, Figs. 4–6; text figs. 181–183

Synonymy

v* 1833	*Pecten strictus* sp. nov; Münster in Goldfuss, p. 49, pl. 91, figs. 4a–c.
1836	*Pecten strictus* Münster; Roemer, p. 69.
v*p 1850	*Pecten Minerva* sp. nov; d'Orbigny, v. 2, p. 54 (Boule, 1932, v. 21, p. 11, pl. 2, fig. 1).
1850	*Pecten Marcus* sp. nov; d'Orbigny, v. 2, p. 54 (Boule, 1932, v. 21, p. 11, pl. 2, fig. 2).
? 1852	*Pecten Beaumontinus* sp. nov; Buvignier, p. 24, pl. 19, figs. 26–30.
1852	*Pecten Dyoniseus* sp. nov; Buvignier, p. 24, pl. 19, figs. 26–30.
? 1859	*Pecten Grenieri* sp. nov; Contejean, p. 311, pl. 23, figs. 7–9.
1860	*Pecten strictus* Münster; Coquand, p. 79.
1860	*Pecten Marcus* d'Orbigny; Coquand, p. 91.
? 1862	*Pecten Banneanus* sp. nov; Étallon in Thurmann and Étallon, p. 259, pl. 36, fig. 12.
? 1862	*Pecten Pagnardi* sp. nov; Étallon in Thurmann and Étallon, p. 259, pl. 36, fig. 12.
1862	*Pecten astartinus* sp. nov; Étallon in Thurmann and Étallon, p. 260, pl. 36, fig. 14.
1862	*Pecten beaumontinus* Buvignier; Thurmann and Étallon, p. 260, pl. 36, fig. 14.
non 1862	*Pecten Grenieri* Contejean; Thurmann and Étallon, p. 265, pl. 37, fig. 7.
1863	*Pecten Minerva* d'Orbigny; Dollfus, p. 80, pl. 14, figs. 4–6.
1864	*Pecten* cf. *strictus* Münster; v. Seebach, p. 98.
? 1867	*Pecten solidulus* Stoppani; J. Meneghini, p. 162, pl. 28, fig. 12.
1872	*Pecten kimmeridgiensis* Cotteau; de Loriol et al., p. 381, pl. 22, fig. 4.
1872	*Pecten Grenieri* Contejean; de Loriol et al., p. 382, pl. 22, figs. 5, 6.
v*? 1872	*Pecten tombecki* sp. nov; de Loriol in de Loriol et al., p. 383, pl. 22, figs. 7–11.
? 1874	*Pecten gioenii* sp. nov; Gemmellaro and Di Blasi, p. 119, pl. 3, figs. 5–7.
? 1875	*Pecten Gioenii* Gemmellaro and Di Blasi; Gemmellaro, p. 50.
1875	*Pecten strictus* Münster; de Loriol and Pellat, p. 190, pl. 22, figs. 10, 15.
? 1878	*Pecten (Chlamys) Veneris* sp. nov; Gemmellaro and Di Blasi in Gemmellaro, p. 396, pl. 30, figs. 11, 12.
1881	*Pecten strictus* Münster; de Loriol, p. 90, pl. 12, fig. 11.
v non 1883	*Pecten* aff. *Grenieri* Contejean; Boehm, p. 603, pl. 67, figs. 17, 18.
v non 1883	*Pecten* aff. *Gioenii* Gemmellaro and Di Blasi; Boehm, p. 604, pl. 67, figs. 19, 20.
1893	*Pecten (Camptonectes)* cf. *Grenieri* Contejean; Fiebelkorn, p. 399, pl. 14, fig. 11.
non 1893	*Pecten beaumontinus* Buvignier; de Loriol, p. 305, pl. 32, fig. 18.
v 1893	*Pecten Minerva* d'Orbigny; de Loriol and Lambert, p. 141, pl. 10, figs. 4–6.
v* 1893	*Pecten sainputeanus* sp. nov; de Loriol in de Loriol and Lambert, p. 143, pl. 10, fig. 9.
? 1904	*Pecten (Chlamys) Girardoti* sp. nov; de Loriol, p. 220, pl. 23, fig. 7.
? 1905	*Pecten (Camptonectes) insutus* sp. nov; Cragin, p. 44, pl. 4, figs. 11, 12.
v?p 1905	*Pecten Minerva* d'Orbigny; Peron, p. 220.
v ? 1905	*Pecten beaumontinus* Buvignier; Peron, p. 230.
1905	*Pecten kimmeridgiensis* Cotteau; Peron, p. 231.
? *1905*	*Pecten (Aequipecten)* cf. *strictus* Münster; Kilian and Guebhard, p. 758.
? 1906	*Pecten fibratus* sp. nov; Fucini, p. 618, pl. 11, fig. 2.
non 1907b	*Chlamys* cf. *stricta* (Münster); Cossmann, p. 2, pl. 2, figs. 5, 6.
1917	*Pecten strictus* Münster; Borissiak and Ivanoff, p. 48, pl. 3, figs. 1, 3.
? 1921	*Chlamys Beaumontina* (Buvignier); Cossmann, p. 6, pl. 1, fig. 1.
? 1931	*Pecten (Aequipecten) arachnoideus* sp. nov; Sokolov and Bodylevsky, p. 61, pl. 4, figs. 10, 11.
v 1936	*Aequipecten Grenieri* (Contejean); Dechaseaux, p. 52, pl. 8, fig. 7.
v non 1936	*Aequipecten Beaumontinus* (Buvignier); Dechaseaux, p. 53, pl. 8, fig. 4.
v 1936	*Aequipecten Minerva* (d'Orbigny); Dechaseaux, p. 53, pl. 7, fig. 22, pl. 8, fig. 1.
1936	*Aequipecten strictus* (Münster); Dechaseaux, p. 54.
1936	*Aequipecten Dionyseus* (Buvignier); Dechaseaux, p. 54.
v 1936	*Aequipecten astartinus* (Étallon); Dechaseaux, p. 55, pl. 8, fig. 5.
(?) 1936	*Aequipecten kimmeridgiensis* (Cotteau); Dechaseaux, p. 55.
1952	*Chlamys minerva* (d'Orbigny); Chavan, p. 35, pl. 2, figs. 12, 13.
(?) *1965*	*Pecten insutus* Cragin; Alencasta de Cserna and Estela Buitron, p. 10.

Lectotype of *Pecten strictus* Münster in Goldfuss 1835, p. 49, pl. 91, figs. 4a–c designated herein; BSPHG AS VII 636 (figs. 4a and 4b of Goldfuss' pl. 91 are probably restored illustrations of this specimen); Pl. 10, Fig. 6 herein; 'Zone of *Pteroceras oceani*' (L. Kimmeridgian), Oelingerberg bei Kappeln, N. Germany. Paralectotypes; BSPHG (3 specimens); also 'Zone of *Pteroceras oceani*', Oelingerberg bei Kappeln.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

'Pecten testa ovato-orbiculari convexo-plana aequivalvi, lineis radiantibus confertis subaequalibus rectis, striis concentricis subtilissimis vix conspicuis, auriculis inaequalibus lineatis.

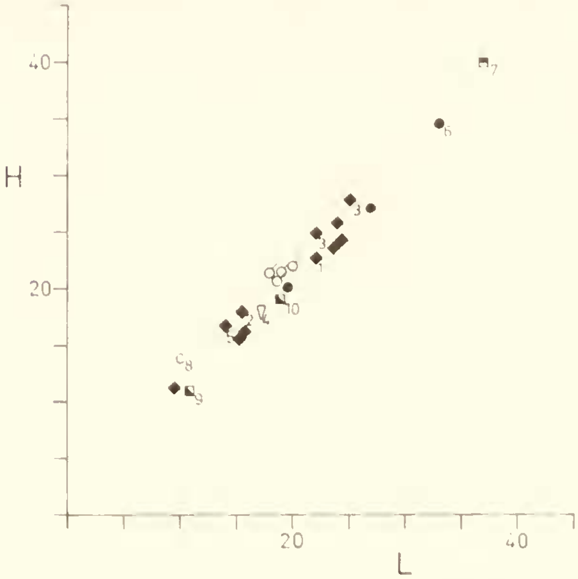
E montibus Westphalicis. M. M.

Eyförmig, flach-convex, gleichklappig, mit gedrängten, sehr zahlreichen, feinen und geraden ausstrahlenden Linien, von welchem einige hier und da etwas dicker erscheinen als die übrigen. Sie sind auch auf den ungleichen Ohren bemerklich, und hier von deutlichen concentrischen Linien durchkreuzt, welche auf der übrigen Schale nur durch Vergröße-rung sichtlich werden.

Kommt mit dem vorigen an demselben Fundorte vor.'

2. AMENDED DIAGNOSIS

Distinguished from *R. vagans* and *R. varians* by the larger number of radial striae and from the latter also by the smaller number of initial plicae. Distinguished from all other species of *Radulopecten* by the existence of a non-plicate phase early in ontogeny.



Text fig. 181: *Radulopecten strictus* – height/length.

3. AMENDED DESCRIPTION

Essentially very similar to *R. varians*. Differing in the maintenance of a sub-ovate form (text fig. 181) to the maximum height of 35 mm (BM unnumbered), in the somewhat higher convexity and slightly smaller byssal notch, in the tendency for the posterior auricles to meet the hinge line at 90°, and in the ornament.

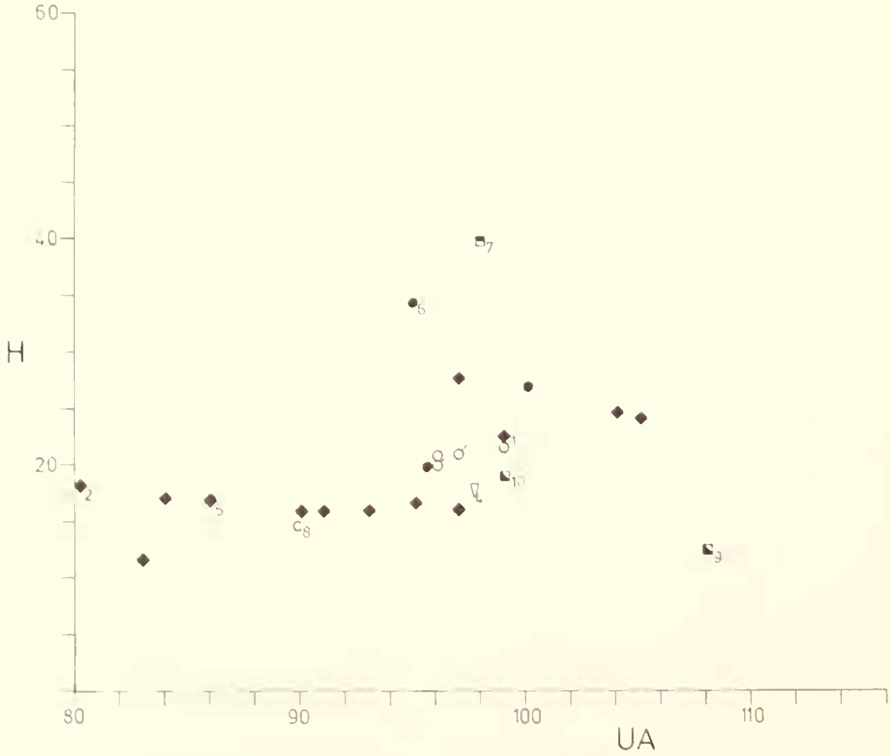
Right valve ornamented with between 73 (MNO) and 110 (BM 25344) radial striae (Pl. 10, Figs. 4, 5); left valve ornamented with between 60 (BM unnumbered) and 75 (MNO) and probably up to 85 (see Section 4) radial striae (Pl. 10, Fig. 6) of which between 5 and 8 and possibly up to 12 (see Section 4) develop into low plicae bearing lamellae at intervals of about 2 mm.

H/UA is plotted in text fig. 182.

4. DISCUSSION

The lectotype (herein designated) of *'Pecten' strictus* Münster (BSPHG AS VII 636; Pl. 10, Fig. 6) is a poorly preserved specimen but the existence of closely spaced radial striae leaves no doubt that it is a representative of the species described in Section 3, for which Münster's name is thus the senior synonym. Kilian and Guebhard's (1905) record of unfigured examples of Münster's species from the Bathonian must be treated with caution owing to the unusual stratigraphic horizon (see Section 5). Cossmann's (1907b) record of Münster's species is discussed under *Chlamys (Ch.) textoria*.

One of the two remaining syntypes of *'P.' Minerva* d'Orbigny (MNO 4725) is clearly referable to *Radulopecten stric-*



Text fig. 182: *Radulopecten strictus* – height/umbonal angle.

tus but the other (MNO 4725B) bears more resemblance to the 'coarse' phenotype of *Ch. (Ch.) textoria.* Some of the specimens (MNP) referred to d'Orbigny's species by Peron (1905) are undoubtedly examples of *R. strictus* but others are more reminiscent of *R. varians.*

The author has been unable to trace the holotype (M) of *'P.' Marcus* d'Orbigny but Boule (1932) has provided a photograph of the specimen which, although poorly preserved, displays the fine radial striae characteristic of *R. strictus.*

The figure of *'P.' Beaumontinus* Buvignier resembles *R. strictus* but the text specifies an abnormally small number of radial striae (50–60) which are said to be raised into plicae on both the left and right valves. Dechaseaux (1936) has figured a specimen (NM) which may be a type of Buvignier's species and this, with more than 15 plicae, is clearly an example of *R. varians.* Specimens referred to Buvignier's species by de Loriol (1893) are similarly referable to *R. varians* and Peron's (1905) specimens (MNP) appear to have only about 35 striae and thus probably also belong in this species. Thurmann and Étallon (1862) figure a right valve with 90–100 striae (within the range of *R. strictus)* under Buvignier's specific name but also appear to use the same specimen as a basis for the erection of a new species, *'P.' astartinus.* Cossmann's (1921) *'Chlamys' Beaumontina* was said to have 60–70 striae on the right valve and therefore seems to occupy an intermediate position between *R. strictus* and *R. varians.*

The figures of *'P.' Dyoniseus* Buvignier closely resemble *R. strictus* and a specimen in NM which may be a type has metric proportions (1) and number of striae on the right valve (100) within the range of the latter species.

The figure of *'P.' Grenieri* Contejean depicts a specimen with many radial striae, as in *R. strictus,* but which is however also ornamented with comarginal lamellae, giving a resemblance to *Camptonectes (Camptochlamys) obscurus.* H/L (2) is within the range of the former species but H/UA is somewhat high. Specimens referred to Contejean's species by de Loriol et al. (1872), Fiebelkorn (1893) and Dechaseaux (1936) are clearly examples of *R. strictus* but specimens referred to Contejean's species by Thurmann and Étallon (1862) and Boehm (1883) have affinities with *C. (Cc.) obscurus.*

It has proved impossible to trace the original description of *'P.' kimmeridgiensis* Cotteau but Peron (1905), who almost certainly examined the type material, has applied the name to specimens from the Kimmeridgian described as having numerous radial striae, which can thus be safely assumed to be examples of *R. strictus.* De Loriol et al. (1872) figure a right valve under Cotteau's name which, with about 90 striae, is indistinguishable from *R. strictus.* Specimens referred to *'Aequipecten' kimmeridgiensis* by Dechaseaux (1936) were allied with *'Ae.' Grenieri* (Contejean) and *'Ae.' astartinus* (Étallon) and are thus very probably conspecific with *R. strictus* (see above).

Although the syntypes of *'P.' tombecki* de Loriol (MNS) have 12 plicae on the left valve the fact that the number of striae (60–70) and H/L (3) is within the range of *R. strictus* suggests that they should be considered to be extreme variants of the latter species.

The original figure of *'P.' gioenii* Gemmellaro and Di Blasi from Sicily depicts a specimen with about 70 striae on the left valve and metric proportions (4) within the range of *R. strictus.* Some doubt must, however, remain over whether *P. gioenii* is synonymous with the latter species owing to the anomalously late stratigraphic horizon (L. Tithonian) and the fact that Boehm (1883), who may have examined the type material, has referred to Gemmellaro and Di Blasi's species a specimen (BSPHG) whose continuous comarginal ornament is unlike that of *R. strictus.*

The sole observed type of *'P.' sainputeanus* de Loriol (MNS B. 03984; Pl. 10, Fig. 4), a right valve, has about 76 radial striae and metric proportions (5) within the range of *R. strictus.*

The number of plicae on the left valve (7–8) and H/L (6) of the original figure of *'P.' ('Chlamys') Girardoti* de Loriol does not allow of a separation from *R. strictus.* The abnormally large number of striae (80) and high H/UA probably represents extreme variation within the latter species. The same can be said of the 85 striae on the left valve and high H/UA (7) of the original figure of *'P.' ('Camptonectes') insutus* Cragin, a species from the U. Jurassic of Texas whose H/L is inseparable from *R. strictus.* Alencasta de Cserna and Estela Buitron's (1965) unillustrated record of *'P.' insutus* from the U. Jurassic of Mexico must be treated with some caution owing to the slight possibility that Cragin's species is not synonymous.

'P.' ('Aequipecten') arachnoideus Sokolov and Bodylevsky from Spitzbergen has 70 striae on the left valve and metric proportions (8) of the original figure within the range of *R. strictus.* However, the stratigraphic horizon (Ryazanian) is anomalously late (see Section 5) and together with the number of striae on the right valve (150) suggests that Sokolov and Bodylevsky's species is probably distinct.

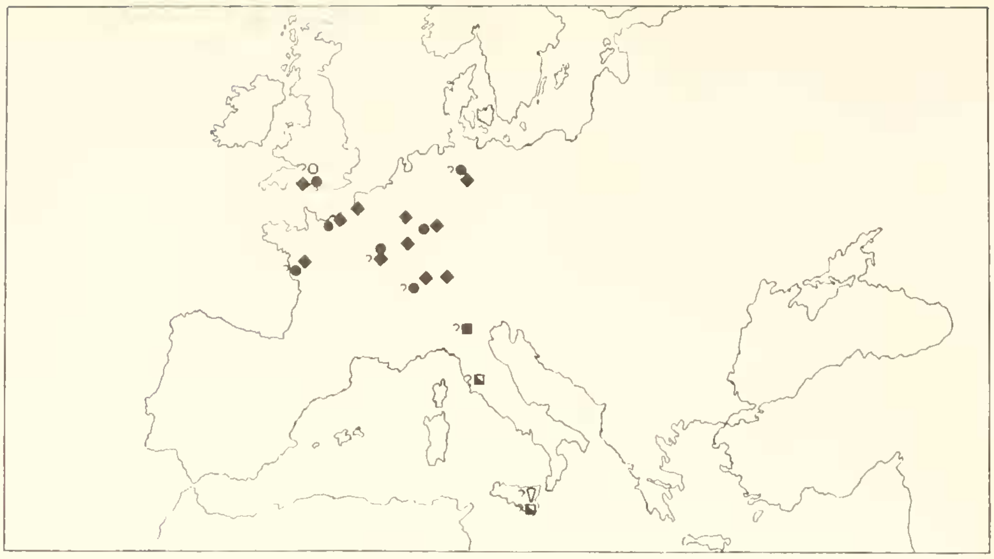
'P.' solidulus Stoppani; J. Meneghini (U. Lias), *'P.' ('Chlamys') Veneris* Gemmellaro and Di Blasi (L. Lias) and *'P.' fibratus* Fucini (L. Lias) are all finely striate forms but their horizons of derivation suggest that they are probably worn specimens of *Ch. (Ch.) textoria* rather than early representatives of *R. strictus.* *'P.' fibratus* also has an unusually low H/UA (9) although H/L in this species and both H/L and H/UA (10) of *'P.' ('Ch.') Veneris* are within the range of *R. strictus.* Stoppani's original description of *'P.' solidulus* has not been traced.

'P.' Banneanus Étallon and *'P.' Pagnardi* Étallon are both discussed under *R. varians.*

5. STRATIGRAPHIC RANGE

The earliest certain occurrences of *R. strictus* are in the Oxfordian and of these none are undoubtedly earlier than the U. Oxfordian. Pre-Oxfordian occurrences of *R. strictus* may be constituted by four poorly preserved specimens (BM unnumbered; identified with a glyph in text figs. 181, 182) from the Kellaways Rock (Callovian) of Wiltshire and by specimens from the Bathonian (Kilian and Guébhard, 1905) and Lias (J. Meneghini, 1867; Gemmellaro, 1878; Fucini, 1906) discussed in Section 4.

The species is locally common in the L. Kimmeridgian but certain U. Kimmeridgian records are restricted to specimens



Text fig. 183: *Radulopecten strictus* – European distribution.

mentioned in de Loriol et al. (1872) and de Loriol and Pellat (1875).

Specimens from the L. Tithonian of Sicily (Gemmellaro and Di Blasi, 1874; Gemmellaro, 1875) may perhaps be late representatives of *R. strictus* and there is a slim possibility that specimens from the Ryazanian of Spitzbergen (Sokolov and Bodylevsky, 1931) may constitute yet later examples of the species (see Section 4).

6. GEOGRAPHIC RANGE

The distribution of *R. strictus* is centred in N. W. Europe (text fig. 183). The only possible occurrences (see Section 4) outside this area are in the L. Tithonian of Sicily (Gemmellaro and Di Blasi, 1874; Gemmellaro, 1875) and the U. Jurassic of Texas (Cragin, 1905) and Mexico (Alencasta de Cserna and Estela Buitron, 1965).

7. DESCRIPTION OF ECOLOGY

R. strictus occurs commonly in condensed oolitic ironstones of the Pseudocordata zone (U. Oxfordian) near Weymouth, Dorset where it reaches a maximum height of 35 mm (BM unnumbered).

In U. Oxfordian sands in Normandy *R. strictus* is a quite common element in a bivalve fauna dominated by *Neomiodon* and cyprinids but in which trigoniids, astartids, tancrediids and corbulids also occur (Chavan, 1952).

R. strictus is common in the Calcaire à Astartes (Cymodoce zone), a limestone/marl sequence in the E. Paris Basin. It also appears to be quite common in the Kimmeridgian of Normandy and the Boulonnais but the exact horizon within the clay/phosphate nodule sequence is not clear.

R. strictus is not known to be common in any areas apart from those discussed above.

8. INTERPRETATION OF ECOLOGY

During its short acme *R. strictus* was able to colonise a wide variety of level bottom substrates. Tolerance of a range of energy levels is suggested by its occurrence in both arenaceous and argillaceous sediments.

The predominance of brackish water forms (Hallam, 1976) in the U. Oxfordian sands in Normandy indicates that salinities were usually reduced. However, the occurrence of apparently fully marine forms (e. g. trigoniids) suggests that salinities were sometimes normal during deposition of this unit thus the presence of *R. strictus* does not necessarily imply an ability to tolerate reduced salinities.

Assuming that specimens derived from Sicily, Texas and Mexico (see Section 4) are representatives of *R. strictus* and that therefore the species was able to tolerate waters which were warmer than those of the main range in N. W. Europe the absence of *R. strictus* from apparently suitable limestone/marl facies in southern continental Europe (e. g. the Rhone Basin) is a mystery.

A fairly close Recent morphological analogue of *R. strictus* is *Chlamys (Ch.) nivea* (see Tebble, 1976).

9. FUNCTIONAL MORPHOLOGY

Since, in the relevant aspects of morphology *R. strictus* is almost identical to *R. varians*, a similar mode of life, tightly byssate on such hard substrates as shells, can be inferred.

10. ORIGINS AND EVOLUTION

The ancestor of *R. strictus* was almost certainly *R. varians*. The increase in the number of radial striae and decrease in the number of initial plicae cannot have been caused by heterochrony so change in the structural rather than the regulatory genome is perhaps implied.

Within *R. strictus* eurytopy combined with small size and a possible phyletic reduction in maximum height from the U. Oxfordian (H_{max}: 35) to the L. Kimmeridgian (H_{max}: 28; BM L87356) points to the prevalence of 'r' selection (Gould, 1977).

No convincing deterministic explanation is available to account for the post L. Kimmeridgian decline of *R. strictus*.

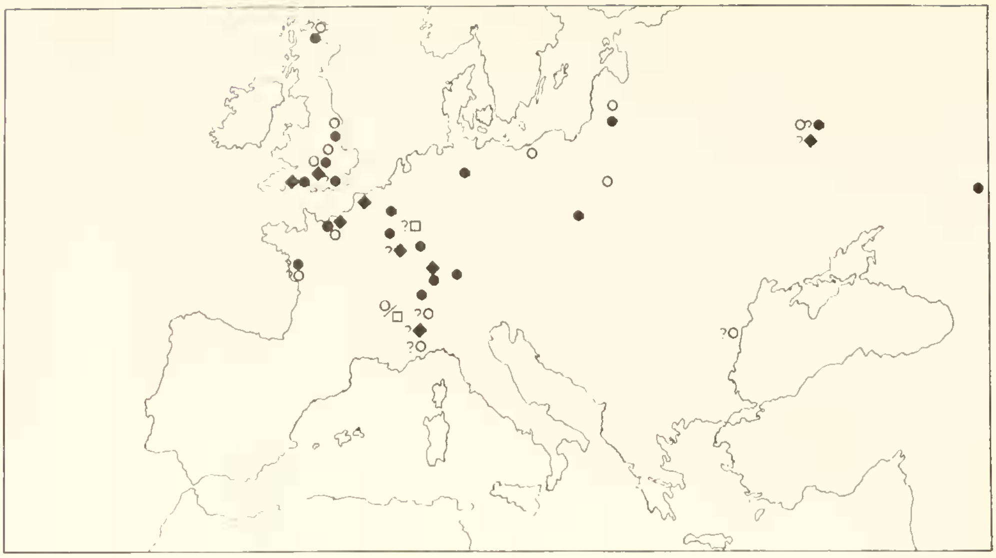
Radulopecten fibrosus (J. Sowerby 1816)

Pl. 10, Figs. 7–18, 20–22, ?Fig. 24; text figs. 184–192

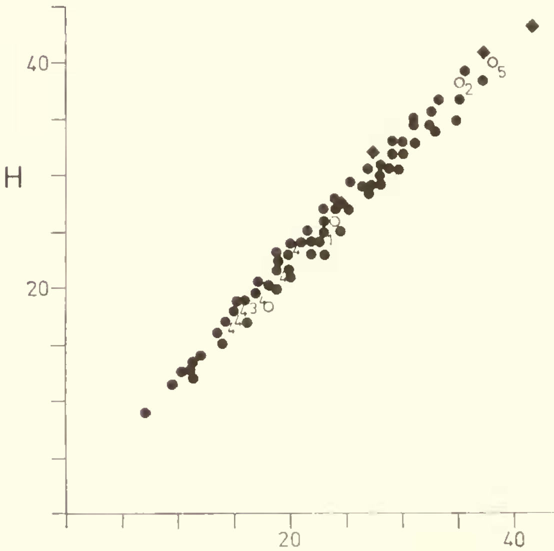
Synonymy

v* 1816	*Pecten fibrosus* sp. nov; J. Sowerby, p. 84, pl. 136, figs. 1, 2.
1822	*Pecten sulcatus* sp. nov; Young and Bird, p. 33, pl. 9, fig. 3.
non 1829	*Pecten fibrosus* J. Sowerby; Phillips, pl. 6, fig. 3.
1831	*Pecten fibrosus* J. Sowerby, Deshayes, p. 82, pl. 8, fig. 5.
1833	*Pecten fibrosus* J. Sowerby; Goldfuss, p. 46, pl. 90, fig. 6.
1836	*Pecten fibrosus* J. Sowerby; Roemer, p. 69.
(?) 1836	*Pecten fibrosus* J. Sowerby; Lamarck, p. 227.
(?) *1839*	*Pecten fibrosus* J. Sowerby; Bean, p. 60.
v non 1850	*Pecten fibrosus* J. Sowerby; d'Orbigny, v. 1, p. 341.
v* 1850	*Pecten subfibrosus* sp. nov; d'Orbigny, p. 373.
non 1852	*Pecten fibrosus* α var. nov; Bronn, p. 211.
1852	*Pecten fibrosus* β var. nov; Bronn, p. 211.
non 1852	*Pecten fibrosus* J. Sowerby; Quenstedt, p. 507, pl. 40, fig. 47.
(?) 1858	*Pecten fibrosus* J. Sowerby; Oppel, p. 568.
? 1859	*Pecten Thurmanni* sp. nov; Contejean, p. 315, pl. 23, figs. 10–12.
non 1860	*Pecten fibrosus* J. Sowerby; Damon, pl. 3, figs. 1, 1a.
1860	*Pecten vagans* J. de C. Sowerby; Damon, pl. 9, fig. 4 (non J. de C. Sowerby sp.).
(?) *1860*	*Pecten fibrosus* J. Sowerby; Coquand, p. 70.
(?) *1860*	*Pecten subfibrosus* d'Orbigny; Coquand, p. 73.
1862	*Pecten subfibrosus* d'Orbigny; Thurmann and Étallon, p. 254, pl. 36, fig. 1.
1862	*Pecten Veziani* sp. nov; Étallon in Thurmann and Étallon, p. 264, pl. 37, fig. 8.
1863	*Pecten Midas* d'Orbigny; Dollfus, p. 79, pl. 14, figs. 1–3 (non d'Orbigny sp.).
1864	*Pecten subfibrosus* d'Orbigny; v. Seebach, p. 96.
(?) 1867	*Pecten fibrosus* J. Sowerby; Laube, p. 12.
? 1872	*Pecten Midas* d'Orbigny; de Loriol et al., p. 385 (non d'Orbigny sp.).
1874	*Pecten fibrosus* J. Sowerby; Brauns, p. 337.
? 1875	*Pecten midas* d'Orbigny; de Loriol and Pellat, p. 193 (non d'Orbigny sp.).
non 1880	*Pecten fibrosus* J. Sowerby; Damon, pl. 3, figs. 1, 1a.
1880	*Pecten vagans* J. de C. Sowerby; Damon, pl. 9, fig. 4 (non J. de C. Sowerby sp.).
v 1880	*Chlamys Midas* (d'Orbigny); Damon, pl. 17, fig. 4 (non d'Orbigny sp.).
1882	*Pecten subfibrosus* d'Orbigny; Roeder, p. 49, pl. 1, figs. 12a–d.
non 1882	*Pecten fibrosus* J. Sowerby; Roeder, p. 50, pl. 1, figs. 11a, 11b.
1883	*Pecten fibrosus* J. Sowerby; Lahusen, p. 23, pl. 2, fig. 3.
1893	*Chlamys subfibrosa* (d'Orbigny); Siemiradzki, p. 119.
1894	*Pecten subfibrosus* d'Orbigny; de Loriol, p. 45.
(?) 1897	*Pecten subfibrosus* d'Orbigny; de Loriol, p. 127.
(?) 1900	*Pecten subfibrosus* d'Orbigny; de Loriol, p. 126.
non 1900	*Aequipecten fibrosus* (J. Sowerby); E. Philippi, p. 98, fig. 15.
non 1901	*Pecten (Chlamys) subfibrosus* d'Orbigny; de Loriol, p. 106.
(?) 1904	*Pecten subfibrosus* d'Orbigny; de Loriol, p. 227.
1904	*Pecten subfibrosus* d'Orbigny; Ilovaisky, p. 251, pl. 8, figs. 14, 15a, 15b.
(?) *1905*	*Pecten fibrosus* J. Sowerby; Kilian and Guébhard, p. 766.
1911	*Pecten subfibrosus* d'Orbigny; Boden, p. 192, pl. 8, fig. 1.
1915	*Pecten subfibrosus* d'Orbigny; Krenkel, p. 299, pl. 26, fig. 23.
? 1915	*Pecten (Aequipecten) Triboleti* sp. nov; Rollier, p. 475, pl. 30, fig. 11.
v non 1916	*Pecten fibrosus* J. Sowerby; Douville, p. 74, pl. 10, figs. 1a, 1b.
1917	*Pecten subfibrosus* d'Orbigny; Borissiak and Ivanoff, p. 28, pl. 4, figs. 7, 8, 9a, 9b, 12–14.
1917	*Pecten vagans* J. de C. Sowerby; Borissiak and Ivanoff, p. 33, pl. 4, fig. 6 (non J. de C. Sowerby sp.).
1917	*Pecten Sokolowi* sp. nov; Borissiak and Ivanoff, p. 46, pl. 2, figs. 10, 10a.
(?) *1925*	*Pecten fibrosus* J. Sowerby; Read et al., p. 80.
v 1926	*Aequipecten fibrosus* (J. Sowerby); Arkell, p. 546, pl. 34, figs. 2–5.
v 1931a	*Chlamys (Aequipecten) fibrosa* (J. Sowerby); Arkell, p. 112, pl. 11, figs. 6–12.
v* 1931a	*Chlamys (Aequipecten) superfibrosa* sp. nov; Arkell, p. 114, pl. 11, figs. 13–16.
pv 1931a	*Chlamys (Aequipecten) midas* (d'Orbigny); Arkell, p. 115, pl. 11, figs. 17–21 (non d'Orbigny sp.).
1934	*Pecten (Aequipecten) fibrosus* J. Sowerby; Stoll, p. 21, pl. 2, fig. 19.
1934	*Pecten (Aequipecten) fibrosus* var. *duplicostatus* var. nov; Stoll, p. 21, pl. 2, figs. 16–18.
1934	*Pecten (Aequipecten) tenuicostatus* sp. nov; Stoll, p. 22, pl. 2, fig. 20.
v 1936	*Aequipecten fibrosus* (J. Sowerby); Dechaseaux, p. 47, pl. 6, figs. 17, 17a; ?pl. 6, figs. 15, 16, 16a (non pl. 6, figs. 18, 18a, 19, 20, pl. 7, figs. 1–3).
? 1936	*Aequipecten Thurmanni* (Contejean); Dechaseaux, p. 57.
1936b	*Chlamys fibrosa* (J. Sowerby); Arkell, p. 88.
1952	*Chlamys (Aequipecten) fibrosa* (J. Sowerby); Makowski, p. 17.
1952	*Chlamys (Radulopecten) fibrosa* (J. Sowerby); Chavan, p. 36, pl. 2, fig. 14.
? 1952	*Chlamys (Radulopecten) qualicosta* (Étallon); Chavan, p. 37, pl. 2, fig. 15 (non Étallon sp.).
v*? 1956	*Chlamys (Radulopecten) drewtonensis* sp. nov; Neale, p. 371, pl. 28, figs. 1–5.
(?) *1971*	*Aequipecten fibrosus* (J. Sowerby); Barbulescu, p. 227.
(?) *1971*	*Chlamys (Radulopecten) fibrosa* (J. Sowerby); Worssam and Ivimey-Cook, p. 40.
pv 1978	*Chlamys (Radulopecten) fibrosa* (J. Sowerby); Duff, p. 72, pl. 6, figs. 2, 7–9; text fig. 24.
v? 1978	*Chlamys (Radulopecten) drewtonensis* Neale; Duff, p. 208, pl. 6, figs. 3, 4.

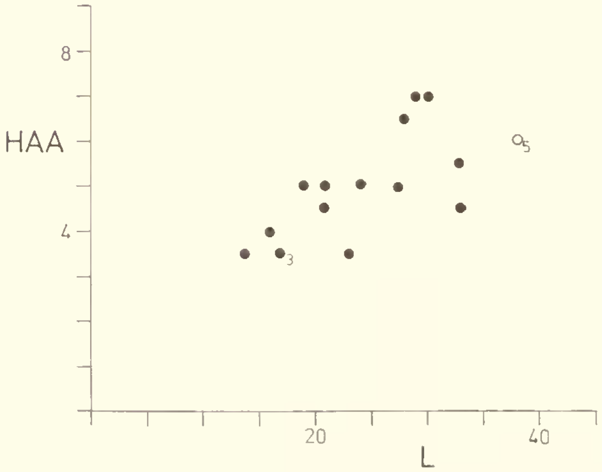
Lectotype of *Pecten fibrosus* J. Sowerby 1816, p. 84, pl. 136, fig. 2 designated Arkell, 1931a, p. 114; BM 43305 (the original to the left hand figure of J. Sowerby's pl. 136, fig. 2); Pl. 10, Fig. 21 herein; H: 25, L: 23.5, I_R: 11, UA: 95; Corallian (Oxfordian), Oxford. Paralectotype; BM 43306 (the original to the right hand figure of J. Sowerby's pl. 136, fig. 2); Pl. 10, Fig. 20 herein; Kellaways Beds (L. Callovian) fide Arkell (1931a), Chatley, Somerset.



Text fig. 184: *Radulopecten fibrosus* – European distribution.



Text fig. 185: *Radulopecten fibrosus* – height/length.



Text fig. 186: *Radulopecten fibrosus* – height of anterior auricle/length.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

'Depressed, orbicular, with a rectangular beak, nine or ten broadish diverging grooves and numerous sharp concentric striae; ears equal, rectangular; margin undulated internally.

Rather longer than broad; the back is formed of two straight lines meeting at an angle, sometimes greater, but seldom less than a right angle; the undulations within the margin are regular and rather deep. The striae are composed of small very prominent sharp ridges that hold the shell firmly to the stone in which it lies.

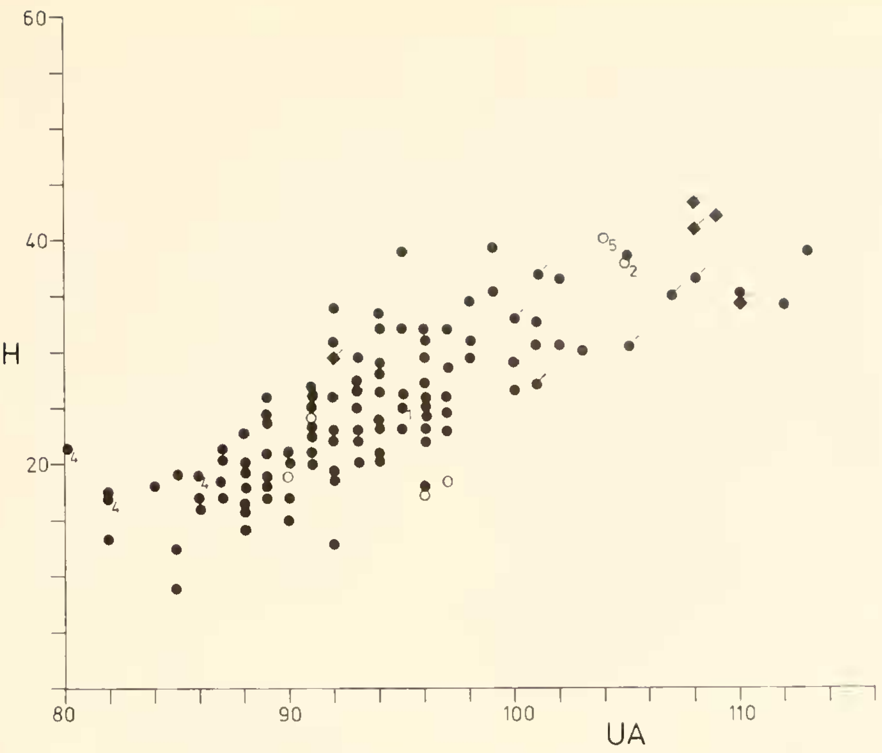
This is remarkable at first sight for its broad and few sulci, and for all the fine undulating transverse striae all over them. I have but seldom seen it in pairs but Mr. Strangeways has a pair from Carrington, Oxfordshire, and I have an excellent specimen from the Chatley Cornbrash, by favour of T. Meade, esq. and a small one showing the inside from Oxfordshire. These last two are figured. Mr. Mantell was so kind as to send me one from North Leach, Gloucestershire, which has only 9 costae, and Mrs. Gent has met with something similar, but plainer at Kellaways; if these should prove to be different species, I shall notice them again.'

2. AMENDED DIAGNOSIS

Distinguished from *R. scarburgensis* by the lack of radial striae, from *R. inequicostatus* by the larger number of plicae, from *R. sigmaringensis* by the lamellose rather than spinose ornament and from all other species of *Radulopecten* by the lack of a non-plicate zone.

3. AMENDED DESCRIPTION

Disc sub-ovate, higher than long, growing allometrically (text fig. 185) to become more orbicular near the maximum height of 43.5 mm (BM L42148). Umbonal angle increasing during ontogeny but relatively invariant at any one size (text fig. 187). Disc flanks low.



Text fig. 187: *Radulopecten fibrosus* – height/umbonal angle.

Equilateral, inequivalve, low convexity, left valve more convex than right. Intersinal distance greater in left valve than right, increasing with approximate isometry in both (text figs. 188, 189). Byssal notch depth variable, small to moderate.

Auricles well demarcated from disc, variable in size, anterior larger than posterior. All auricles meeting hinge line at about 90°. Anterior auricle of right valve meeting disc at about 90°, remaining auricles meeting disc at an acute angle. All auricles ornamented with closely spaced comarginal striae.

Height of anterior auricle (text fig. 186) and lengths of anterior and posterior auricles (text figs. 190, 191) variable.

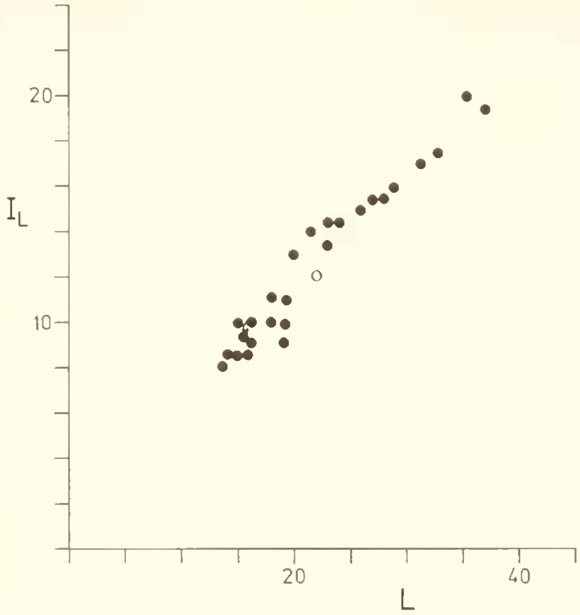
Left valve ornamented with between 10 and 13, usually 11, original plicae (text fig. 192), narrower than sulci. Height of plicae variable, usually moderately high in early representatives (e. g. Pl. 10, Fig. 8) but uniformly low in late forms (e. g. Pl. 10, Figs. 13, 16–18). Additional low plicae intercalated during ontogeny of forms with original plicae to give a maximum total number of 27 (BM 35563). Rate of intercalation apparently faster in some of the latest representatives (see Section 7). Forms with low plicae bearing evenly spaced comarginal lamellae on all parts of disc. Comarginal lamellae restricted to plical crests in forms with high plicae.

Right valve usually bearing one less plica than left, with plicae wider than sulci and all parts of disc ornamented with closely spaced comarginl striae.

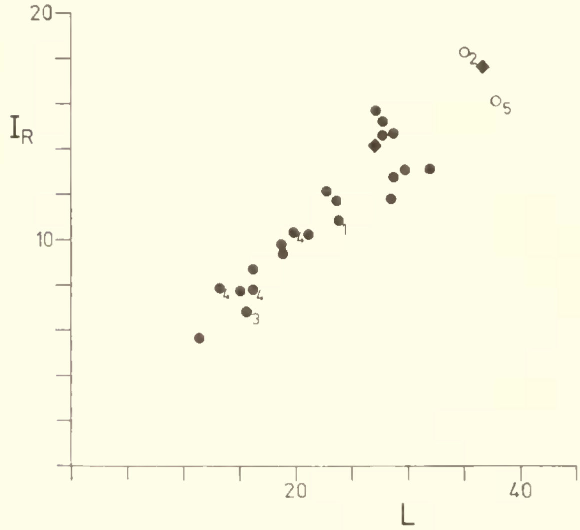
Shell thickness moderate in early representatives, low in later forms (see Section 7).

4. DISCUSSION

Of the two syntypes of *'Pecten' fibrosus* J. Sowerby one (BM 43305; Pl. 10, Fig. 21) is seen only from the interior and the other (BM 43306; Pl. 10, Fig. 20) is poorly preserved. Metric proportions (1) and general shape of the former, designated as lectotype by Arkell (1931a), are, however, indistinguishable from the species described in Section 3 and since J. Sowerby's name is the earliest available for this species it is known hereinafter as *Radulopecten fibrosus*. The second syntype (paralectotype) has metric proportions (2) within the range of *R. fibrosus* and the shape of the auricles confirms that it is a member of the latter species. The superficial similarity of the disc ornament in this specimen to that of *R. scarburgensis* (Young and Bird) is presumably the reason for Phillips' (1829) misapplication of J. Sowerby's specific name to an example of Young and Bird's species. Perhaps through following Phillips' rather than J. Sowerby's usage of *'P.' fibrosus*, d'Orbigny (1850) applied this name to specimens (MNO 3397) of *R. scarburgensis* and saw fit to erect a new species, *'P.' subfibrosus*, for specimens (MNO 3754; Pl. 10, Fig. 22) which are in fact typical representatives of J. Sowerby's species. Other authors (Damon, 1860, 1880; Roeder, 1882; Douville, 1916; Dechaseaux, 1936, pl. 6, figs. 18, 18a, 19, pl. 7, fig. 1) have also applied J. Sowerby's specific name to examples of *R. scarburgensis* so with the evident possibility of misinterpretation of his hypodigm inadequately characterised records of his species in Lamarck (1836), Bean (1839), Oppel (1858), Coquand (1860), Laube (1867), Terquem and Jourdy (1869), Kilian and Guébhard (1905), Read et al. (1925), Barbulescu (1971) and Worssam and Ivimey-Cook (1971) can only be tentatively synonymised. Although most subsequent usages of *'P.' subfibrosus* have been for forms which are undoubtedly within d'Orbigny's hypodigm (= *R. fibrosus*), de Loriol (1901) describes under *'P.' ('Chlamys') subfibrosus* specimens which are almost certainly representative of *R. scarburgensis*. Doubt must therefore be cast on the affinities of unfigured specimens referred to d'Orbigny's species by the same author in 1897, 1900 and 1904, although those described in 1894 do appear to belong to *R. fibrosus*. Coquand's (1860) record of '*P.*' *subfibrosus* is accompanied by neither a figure nor a description so it can only be tentatively synonymised. Bronn (1852) followed d'Orbigny's interpretation of J. Sowerby's hypodigm but considered that specimens such as those forming the basis for '*P.*' *subfibrosus* could only be distinguished at the varietal level. Thus forms belonging to *R. scarburgensis* were referred to as '*P. fibrosus* α and forms belonging to *R. fibrosus* were referred to as '*P.*' *fibrosus* β. Stoll's (1934) variety *duplicostatus* is nothing more than the quite common form of *R. fibrosus* in which intercalation of additional plicae has occurred.



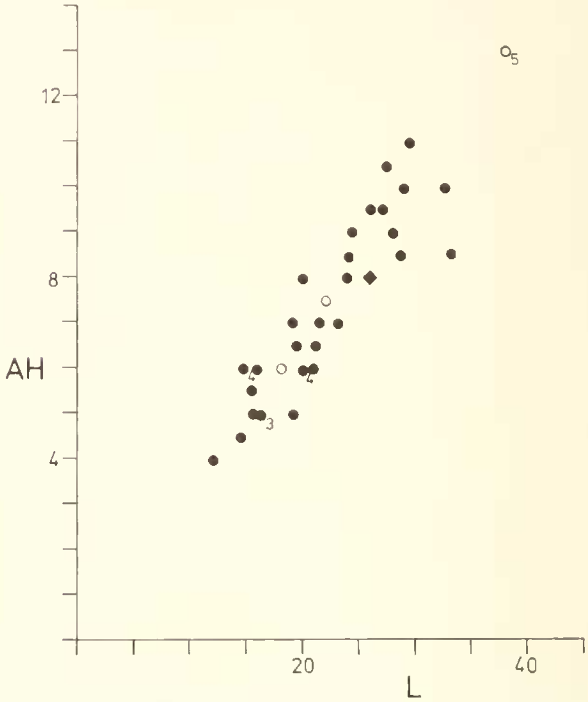
Text fig. 188: *Radulopecten fibrosus* – intersinal distance on left valve/length.



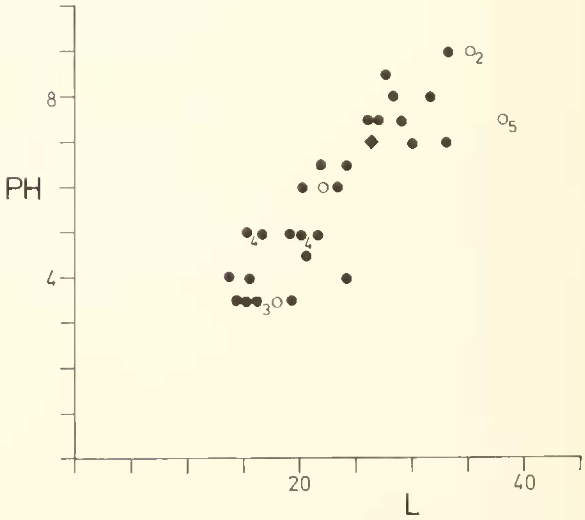
Text fig. 189: *Radulopecten fibrosus* – intersinal distance on right valve/length.

Quenstedt's (1852) and E. Philippi's (1900) misapplication of J. Sowerby's specific name to specimens of *R. vagans* is discussed under the latter species. Certain specimens illustrated by Dechaseaux (1936, pl. 6, fig. 20, pl. 7, figs. 2, 3) under '*Aequipecten*' *fibrosus* may also be referable to *R. vagans* although the horizon (Oxfordian) suggests that they more probably belong in *R. inequicostatus*. Specimens illustrated under '*P.*' *vagans* by Damon (1860, 1880) and Borissiak and Ivanoff (1917) are clearly representative of *R. fibrosus*.

'*P.*' *sulcatus* Young and Bird and *P.* ('*Ae.*') *tenuicostatus* Stoll, both with 11–12 original plicae, are typical early representatives of *R. fibrosus*. The figured specimen of '*P.*' *Vezzani* Étallon (3) and the syntypes of *Ch.* ('*Ae.*') *superfibrosa* Arkell (OUM J8247–8252; Pl. 10, Figs. 11, 12; 4) are small late representatives with rather extreme depression of the plicae. Large late representatives of *R. fibrosus* with the characteristic numerous low plicae were incorrectly referred to '*P.*' *Midas* d'Orbigny (a junior synonym of *Camptonectes* (*C.*) *auritus*) by Dollfus (1863) and this misusage of d'Orbigny's specific name has been perpetuated by Damon (1880)



Text fig. 190: *Radulopecten fibrosus* – anterior hinge length/length.



Text fig. 191: *Radulopecten fibrosus* – posterior hinge length/length.

and Arkell (1931a). It may therefore be that inadequately characterised specimens referred to d'Orbigny's species in de Loriol et al. (1872) and de Loriol and Pellat (1875) are in fact representatives of *R. fibrosus*.

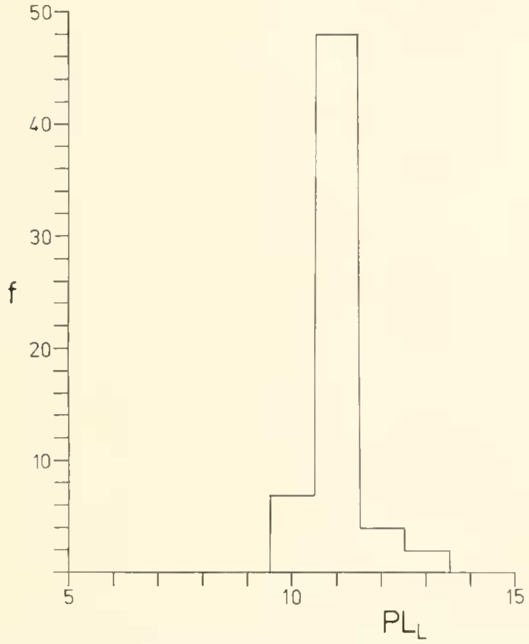
The holotype (OD) of *'Ch.' (R.) drewtonensis* Neale (BM 88737; Pl. 10, Fig. 24) has 13 plicae and most metric proportions (5) within the range of *R. fibrosus*. However, the byssal notch is abnormally large and may indicate that Neale's specimen is indeed a member of a different species. Nevertheless the paucity of comparable specimens makes it more likely that *'Ch.' (R.) drewtonensis* represents extreme variation within *R. fibrosus*.

'Ch.' (R.) qualicosta Étallon; Chavan has irregular plicae but seems to be nearer *R. fibrosus* than Étallon's species (= *R. varians*).

'P.' ('Ae.') Triboleti Rollier was compared with *'P.' fibrosus* but the figured specimen is too poorly preserved to allow confident assignment to any species.

The affinities of *'P.' Thurmanni* Contejean are discussed under *R. vagans*.

'P.' Sokolowi Borissiak and Ivanoff (erected for a form with 13 plicae which is inseparable from *R. fibrosus*) must be rejected as a junior primary hononym of *'P.' Sokolowi* Retowski (? = *Propeamussium (P.) nonarium* q. v.).



Text fig. 192: *Radulopecten fibrosus* – frequency distribution for number of plicae on left valve.

5. STRATIGRAPHIC RANGE

There are no unequivocal records of *R. fibrosus* before the Callovian. Quenstedt's (1852) record of *'P.' fibrosus* from the Bathonian in fact refers to *R. vagans* while Terquem and Jourdy's (1869) Bathonian record of *'P.' fibrosus* is based on unfigured and therefore questionably conspecific specimens (see Section 4). The paralectotype (BM 43306), originally said to be from the Cornbrash (partly Bathonian), is more probably from the Kellaways Beds (Arkell, 1931a) and it seems likely that a specimen in the GPIG labelled 'Cornbrash, St. Etienne' is from the L. Callovian (Macrocephalus zone) part of that formation, the horizon at which *R. fibrosus* first occurs in Yorkshire (e. g. YM 592) and Pomerania (Stoll, 1934). In the former area the species is quite common in the Calloviense zone and the M. Callovian Coronatum zone. In the intervening Jason zone a few specimens are known from central England (Duff, 1978) and *R. fibrosus* seems to be fairly common at this horizon in the Moscow Basin (Lahusen, 1883) and Lithuania (Krenkel, 1915). The last two authors also cite material from the U. Callovian as do Borissiak and Ivanoff (1917) from central Russia and Stoll (1934) from Pomerania. Makowski's (1952) record of *R. fibrosus* from the Callovian of Poland is probably from the upper substage.

In the L. Oxfordian definite records from the Mariae zone are restricted to a few specimens from Yorkshire (author's collection). In the Cordatum zone the species is however abundant and widespread, continuing thus through the Plicatilis zone and almost certainly also the Transversarium zone (U. Oxfordian). Specimens from the Normandy coast and Dorset are the only definite record of *R. fibrosus* in the Cautisnigrae zone; the specimens are nevertheless numerous. Material described by Roemer (1836) and Brauns (1874) from the coralliferous beds of the U. Oxfordian in N. W. Germany may possibly include some specimens from the Cautisnigrae zone since the Middle Coralline Oolite is apparently of this age (Arkell, 1956: 139). Some of Roemer's material was derived from the upper 'Coral Rag' which could well be of Decipiens zone age (Arkell, 1956: 139). These specimens are certainly at least as young as the earliest populations of *R. fibrosus* with depressed plicae seen in Dorset (see Section 7). Since Roemer did not consider it appropriate to apply any specific name other than *'P.' fibrosus* J. Sowerby (syntypes with high plicae) to these specimens, it may be that they exhibit the high plicae characteristic of earlier populations. If so there would be clear evidence that forms with low plicae arose by splitting rather than phyletic change and it would be necessary to accord them a separate specific name (cf. p. 11). Roemer, however mentions specimens with very low plicae in his description of *'P. fibrosus'* and it could be that his material from the upper 'Coral Rag' is the source of this comment. Thus, pending examination of the material, the author prefers to adopt the view that the evolution of forms with low plicae took place phyletically and that they should therefore be referred to as *R. fibrosus*.

R. fibrosus is common and occurs widely in N. W. Europe in the Pseudocordata zone. L. Kimmeridgian records are however restricted to a few specimens from S. England (OUM J2363; BM L19919, L42148, L73018), and specimens from NW. (BM 25921, 33047, LL13479; Dollfus, 1863) and E. (Thurmann and Étallon, 1862) France. The latest zonally defined example is from the Cymodoce zone (BM L42148).

6. GEOGRAPHIC RANGE

R. fibrosus was essentially a Boreal species probably because of the widespread development of argillaceous facies (see Section 8) in the Tethyan region. Certain occurrences of the species are restricted to north-west, north, central and north-east Europe (text fig. 184) and are strongly correlated with the development of arenaceous facies. The restriction of the range to E. Europe during the U. Callovian (see Section 5) cannot be explained by a lack of arenaceous facies elsewhere. At least in Yorkshire apparently suitable sediments (Hackness Rock) are well developed. However, in the latter area *R. scarburgensis* is common and it may be that the latter competitively excluded *R. fibrosus* (see Section 8).

The great reduction in population size which apparently occurred in the Cautisnigrae zone has no obvious explanation.

7. DESCRIPTION OF ECOLOGY

R. fibrosus first occurs commonly in the Kellaways Rock (Calloviense zone) of Yorkshire where it reaches a maximum height of 25 mm (author's collection). The sediments are sandstones, partly oolitic, containing a rather low diversity benthic fauna dominated by the bivalves *Entolium (E.) corneolum*, *Pinna*, *Meleagrinella* and *Modiolus*. A similar sedimentary and faunal association characterises occurrences in the Langdale Beds (Coronatum zone) of the same area and apart from Borissiak and Ivanoff's (1917) record from clay and Makowski's (1952) record, possibly from clay, all occurrences in the Callovian of N. E. Europe (see Section 5) are known to be associated with similar sediments. Elsewhere *R. fibrosus* is rare in the Callovian although it is widespread in the L. and M. Callovian (see Section 5). A height of 37 mm is attained in the L./M. Callovian of Pomerania (Stoll, 1934). The great majority of Callovian specimens of *R. fibrosus* have elevated plicae.

In the Oxfordian of Britain specimens with elevated plicae are abundant in the calcareous sandstones of the Cordatum zone (L. Calcareous Grit), where they reach a maximum height of 26.5 mm (SbM), in biosparites of the Plicatilis zone (e. g. '*Trigonia*' *hudlestoni* Bed [Pl. 10, Fig. 15], Shell-cum-Pebble Bed), where they reach a maximum height of 36.5 mm (OUM J9060), and in contemporaneous oolites (Hambleton and Malton Oolites). Examples of *R. fibrosus* with elevated plicae also occur in oolites in the Transversarium zone of Dorset ('Qualicosta' Bed). However, they are outnumbered 3:1 by specimens of *R. varians*. In marly oolites in the Cautisnigrae zone of the same area (in the '*Trigonia*' *clavellata* Beds) *R. fibrosus* outnumbers *R. varians* 2:1, but both species are common. The great majority of specimens of the former species have low, albeit numerous, plicae (e. g. Pl. 10, Figs. 11, 12). The maximum height is 32 mm (author's collection). The associated fauna, as in L. and M. Oxfordian occurrences of *R. fibrosus*, is dominated by oysters and *Myophorella*. The fauna of sands in the Pseudocordata zone of Dorset (Sandsfoot Grit) where *R. fibrosus* is abundant, is dominated by *Pinna* (association B of Fürsich, 1977) and is very reminiscent of Callovian occurrences of *R. fibrosus*. The maximum height attained is 39 mm (BM L84954). All specimens have thin shells with low plicae and the intercalary plicae appear to be added at a faster rate compared to earlier representatives (e. g. Pl. 10, Fig. 17, cf. also Figs. 13, 16).

R. strictus may be an associate in L. Kimmeridgian occurrences in France (see Section 5). In this substage *R. fibrosus* reaches a maximum height of 41 mm (BM L73018) in the Baylei zone and 43.5 mm (BM L42148) in the Cymodoce zone. Ornamentation is as in the Pseudocordata zone.

Apart from those instances discussed above *R. fibrosus* is only known to be common in the Cordatum zone of Alsace (Roeder, 1882) and in the 'Oxfordian' of Normandy (MNO). Other isolated records appear to be mainly derived from coarse-grained sediments and the only occurrences of more than a few specimens in argillaceous facies are in the Nothe Clay (Plicatilis zone) and Clay Band (Cautisnigrae zone) of Dorset (author's collection).

R. fibrosus only occurs commonly with *R. scarburgensis* in the Cordatum zone of Alsace.

8. INTERPRETATION OF ECOLOGY

It is clear from Section 7 that the high energy environment of arenaceous sedimentation was favourable to *R. fibrosus*.

The general rarity of *R. fibrosus* in argillaceous sediments could be due to competitive inferiority to *R. scarburgensis*, which is widespread in such sediments, rather than to an actual dislike of low energy depositional environments. Evidence for the latter view is provided by the local occurrence of numbers of *R. fibrosus* in clay horizons where *R. scarburgensis* is absent (Nothe Clay, Clay Band). The occurrence of numerous examples of *R. fibrosus* together with *R. scarburgensis* in the Cordatum zone of Alsace seems however to argue against any competitive reaction between the species. Nevertheless, it may be that the two species are derived from different horizons within the zone thus a lack of competition is not proven.

Competitive inferiority to *R. varians* is perhaps suggested by the relative rarity of *R. fibrosus* in association with this species in apparently suitable sediments in the Transversarium zone. However it should be borne in mind that the shells have undoubtedly been transported and that the present disparity in numbers may not reflect the original situation. If competition is inferred in the Transversarium zone the common occurrence of both *R. fibrosus* and *R. varians* in the Cautisnigrae zone of Dorset must be taken to imply a subsequent suppression of competition by niche partitioning.

There is little evidence of competition with *R. strictus*, a probable descendant of *R. varians*.

The size and morphology of *R. fibrosus* seems to be unrelated to environment.

9. FUNCTIONAL MORPHOLOGY

Although the byssal notch is sometimes shallow, the small to moderate adult size allows that *R. fibrosus* could have been byssally attached throughout ontogeny. The reduced ornamentation of the right valve is paradigmatic for tight fixation. The depressed plication of the left valve characteristic of later populations of *R. fibrosus* is also paradigmatic for byssal fixation (on hard substrates) but it would have reduced the strength of the shell and consequently its ability to withstand predatory attacks. Since depression of the plicae results in greater streamlining it is additionally paradigmatic for swimming whereby, moreover, it is possible to avoid predation in a way other than by simply offering passive resistance. It may be that later populations of *R. fibrosus* moved into a new niche to avoid competition with *R. varians* and adoption of the free-living mode of life postulated above (contrasting with the byssate mode of life of *R. varians*) may have been the relevant move. In inferring adaptive value for the morphology of later forms of *R. fibrosus* on the basis of the above argument it should be borne in mind that the evidence for competition between *R. fibrosus* and *R. varians* (in the Transversarium zone) is very weak (see Section 8) and that if the species did not compete it cannot be inferred that there was subsequent niche partitioning.

10. ORIGINS AND EVOLUTION

The most likely ancestor for *R. fibrosus* is *R. vagans* and since the first occurrence of the former is within the geographic range of the latter the possibility of sympatric speciation cannot be ruled out. *R. fibrosus* can be viewed as the product of 'genetic assimilation' and heterochronic acceleration in variants of *R. vagans* with 10–13 initial plicae (cf. *R. varians*). Such variants are, however, uncommon so simple regulatory changes, as implied by the above, may not have been the sole cause of evolution.

The lower mean plical height characteristic of Cautisnigrae zone and later populations of *R. fibrosus* is a reflection not only of the loss of forms with elevated plicae but also of the addition of forms with lower plicae than even the most extreme representatives (e. g. Pl. 10, Fig. 10) of earlier populations. Evolution must therefore have involved some addition to the gene pool.

On the basis of a specimen (Pl. 10, Fig. 7) from a loose block with relatively high plicae, the author previously concluded (JOHNSON, 1980) that mean plical height was slightly greater in the Cautisnigrae zone than in the later Pseudocordata zone. A somewhat protracted episode of evolution in *R. fibrosus* would thus have been evinced (spanning several zones). However, re-examination of the specimen's matrix suggests that it may well be derived from the 'Qualicosta' Bed (Transversarium zone) thus there may have been no change in mean plical height between the Cautisnigrae and Pseudocordata zones. Evidence that evolution in *R. fibrosus* was indeed compressed into a short period of time is supplied by material from Linton Hill, Abbotsbury, Dorset. Here forms with elevated plicae (recorded as *'Chlamys' fibrosa)* were recovered by ARKELL (1936b: 88) from the Sandy Block (uppermost Transversarium zone) while the author has recovered a specimen with low plicae from a horizon only 2m higher (in ARKELL's bed 5).

The fact that the reduction in the plical height of *R. fibrosus* apparently occurred at the very end of the Transversarium zone argues against any idea of change as a response to the (rather earlier) appearance of *R. varians* and thus renders implausible the adaptive explanation advanced in Section 9. The alternative explanation, that change was through genetic drift and involved no increase in the level of adaptation, must be considered reasonable because *R. fibrosus* apparently suffered a population crash (as would promote change through genetic drift) at the time of evolution (see Section 5).

It is possible that the apparent increase in the rate of plical intercalation between the Cautisnigrae and Pseudocordata zones is an illusion created by the larger size of specimens from the latter zone. Even if it is real it is a much less marked change than the slightly earlier reduction in plical height. The reduction in shell thickness in the Pseudocordata zone could well be a product of $CaCo_3$ dissolution in the porous sandstones of this zone.

Although *R. fibrosus* exhibits an overall phyletic increase in maximum height the pattern of change from 25 mm (L. Callovian; ?37 mm [STOLL, 1934]) to 26.5 mm (L. Oxfordian) to 36.5 mm (M. Oxfordian) to 32 mm (U. Oxfordian, Cautisnigrae zone) to 39 mm (U. Oxfordian, Pseudocordata zone) to 41.5 mm (L. Kimmeridgian, Baylei zone) to 43.5 (L. Kimmeridgian, Cymodoce zone) is somewhat oscillatory.

The decline and extinction of *R. fibrosus* in the Kimmeridgian may relate to the widespread development of argillaceous facies (see Section 8).

Radulopecten scarburgensis (YOUNG and BIRD 1822)

Pl. 10, Figs. 23, 25–29, ?Fig. 19, ?Pl. 11, Figs. 1, 3;
text figs. 193–200

Synonymy

1822	*Pecten Scarburgensis* sp. nov; YOUNG and BIRD, p. 234, pl. 9, fig. 10.
1829	*Pecten fibrosus* J. SOWERBY; PHILLIPS, pl. 6, fig. 3 (non J. SOWERBY sp.).
v* 1833	*Pecten subarmatus* sp. nov; MÜNSTER in GOLDFUSS, p. 47, pl. 90, fig. 8.
v*? 1833	*Pecten subcancellatus* sp. nov; MÜNSTER in GOLDFUSS, p. 47, pl. 90, figs. 9a–c.
1845	*Pecten discrepans* sp. nov; BROWN, p. 157.
v 1850	*Pecten fibrosus* J. SOWERBY; D'ORBIGNY, v. 1, p. 341 (non J. SOWERBY sp.).
1852	*Pecten fibrosus* α var. nov; BRONN, p. 211 (non J. SOWERBY sp.).
v non 1858	*Pecten subarmatus* MÜNSTER; QUENSTEDT, p. 754, pl. 92, figs. 8, 9.
1859	*Pecten Bavoux* sp. nov; CONTEJEAN, p. 316, pl. 23, fig. 6.
1860	*Pecten fibrosus* J. SOWERBY; DAMON, pl. 3, figs. 1, 1a (non J. SOWERBY sp.).
1862	*Pecten Laurae* sp. nov; ÉTALLON in THURMANN and ÉTALLON, p. 253, pl. 35, fig. 6.
1864	*Pecten* cf. *Laurae* ÉTALLON; v. SEEBACH, p. 98.
1878	*Pecten subarmatus* MÜNSTER; DE LORIOL, p. 158, pl. 22, fig. 2.
1880	*Pecten fibrosus* J. SOWERBY; DAMON, pl. 3, figs. 1, 1a (non J. SOWERBY sp.).
1881	*Pecten subarmatus* MÜNSTER; DE LORIOL, p. 85, pl. 12, figs. 2–4.
1882	*Pecten fibrosus* J. SOWERBY; ROEDER, p. 50, pl. 1, figs. 11a, 11b (non J. SOWERBY sp.).
1894	*Pecten Laurae* ÉTALLON; DE LORIOL, p. 47, pl. 5, fig. 5, pl. 6, fig. 3.
1897	*Pecten Laurae;* ÉTALLON; DE LORIOL, p. 127.
1901	*Pecten (Chlamys) subfibrosus* D'ORBIGNY; DE LORIOL, p. 106 (non D'ORBIGNY sp.).
1904	*Pecten (Chlamys) Laurae* ÉTALLON; DE LORIOL, p. 218.
v 1905	*Pecten Laurae* ÉTALLON; PERON, p. 216.
1910	*Chlamys subarmata* (MÜNSTER); LISSAJOUS, p. 361, pl. 10, fig. 1.
? 1915	*Pecten (Aequipecten)* sp. nov; ROLLIER, p. 470, pl. 31, figs. 1a–c.
1915	*Pecten (Aequipecten) Catharinae* sp. nov; ROLLIER, p. 472, pl. 30, figs. 8–10.
v 1916	*Pecten fibrosus* J. SOWERBY; DOUVILLÉ, p. 74, pl. 10, figs. 1a, 1b (non J. SOWERBY sp.).

1917 *Pecten subinaequicostatus* Kasansky; Borissiak and Ivanoff, p. 40, pl. 2, figs. 2–4.

1917 *Pecten Laurae* Étallon; Borissiak and Ivanoff, p. 44, pl. 2, fig. 1.

1917 *Pecten subarmatus* Münster; Borissiak and Ivanoff, p. 45, pl. 2, figs. 5, 6.

? 1921 *Chlamys articulatus* (Schlotheim); Newton, p. 395, pl. 11, fig. 7 (non Schlotheim sp.).

1926 *Pecten Laurae* Étallon; Roman, p. 193.

1926 *Chlamys subarmata* (Münster); Roman, pp. 194, 196.

p 1926 *Aequipecten subarmatus* (Münster); Staesche, p. 68.

(?) 1926 *Aequipecten subcancellatus* (Münster); Staesche, p. 70.

1933 *Pecten (Aequipecten)* aff. *subarmatus* (Münster); Dietrich, p. 65, pl. 9, fig. 140.

1935a *Chlamys scarburgensis* (Young and Bird); Arkell, p. xiii.

v*? 1936 *Chlamys (Radulopecten) tipperi* sp. nov; Cox, p. 18, pl. 1, figs. 1–5.

v 1936 *Aequipecten fibrosus* (J. Sowerby); Dechaseaux, p. 47, pl. 6, figs. 18, 18a, 19, pl. 7, fig. 1;? pl. 6, figs. 15, 16, 16a; non pl. 6, figs. 17, 17a, 20, pl. 7, figs. 2, 3 (non J. Sowerby sp.).

1936 *Aequipecten Laurae* (Étallon); Dechaseaux, p. 49.

v 1936 *Aequipecten* cf. *Laurae* (Étallon); Dechaseaux, pl. 7, figs. 4, 4a, 5, 5a.

1939 *Chlamys* cf. *Laurae* (Étallon); Stefanini, p. 182, pl. 20, figs. 7, 8.

1948 *Chlamys (Radulopecten) scarburgensis* (Young and Bird); Cox and Arkell, p. 13.

v*? 1952 *Chlamys (Radulopecten) moondanensis* sp. nov; Cox, p. 12, pl. 1, fig. 13, pl. 2, fig. 7.

1958 *Chlamys (Radulopecten) scarburgensis* (Young and Bird); R. Hudson, p. 420.

1965 *Chlamys (Radulopecten?) kinjeleensis* sp. nov; Cox, p. 57, pl. 17, figs. 6a, 6b, 7a, 7b.

1969 *Chlamys scarburgensis* (Young and Bird); J. Hudson and Palframan, p. 394.

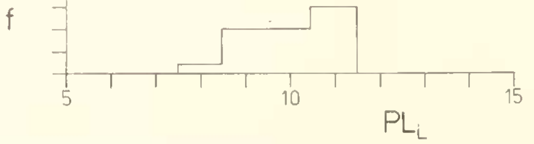
1970 *Aequipecten* cf. *subarmatus* (Münster); Behmel, p. 62.

pv 1978 *Chlamys (Radulopecten) scarburgensis* (Young and Bird); Duff, p. 70, pl. 5, figs. 19, 20, 23, 24, 26, 27, pl. 6, figs. 1, 5, 6.

Neotype of *Pecten Scarburgensis* Young and Bird 1822, p. 234, pl. 9, fig. 10 designated by Duff, 1978, p. 71; SM J12398; figured Duff, 1978, pl. 5, fig. 27; Hackness Rock (U. Callovian), Scarborough, Yorkshire.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

'Fig. 10 represents the inside of a handsome shell, of a larger size and more oblong shape [than '*P.*' *fibrosus* J. Sowerby].from the hard sandstone at the foot of Scarborough Castle. Some specimens are three inches long, but it is very difficult to get any entire. Both valves are convex, and as in No. 12, are closely invested with transverse membranaceous striae, somewhat sharp and rough, crossing both the ribs and the intermediate grooves. There are nine ribs, which are broad and rather flat, but each has an elevated ridge running along the middle of it, surmounted here and there by oblong spines, or sharp scales, crossing the ridge. As this species does not appear to have been hitherto described, we may name it *p. Scarburgensis.*'



Text fig. 193: *Radulopecten scarburgensis* – frequency distribution for number of plicae on left valve.

2. AMENDED DIAGNOSIS

Distinguished from *R. fibrosus* by the presence of radial striae, from *R. sigmaringensis* by the presence of comarginal lamellae rather than spines, from *R. inequicostatus* by the equality of the initial plicae and from all other species of *Radulopecten* by the lack of a non-plicate zone.

3. AMENDED DESCRIPTION

Essentially similar to *R. fibrosus,* differing by the larger maximum height (92 mm, MNP; possibly 170 mm, see Section 4), more variable umbonal angle (text fig. 195), somewhat greater convexity, and tendency for the right valve to be the more convex, by the more equal-sized auricles and tendency for all the auricles to meet the hinge-line at an acute angle and of the anterior auricle of the right valve to meet the disc at an obtuse angle, by the generally smaller byssal notch and by the ornament of the disc (other metric proportions plotted in text figs. 194, 196–8).

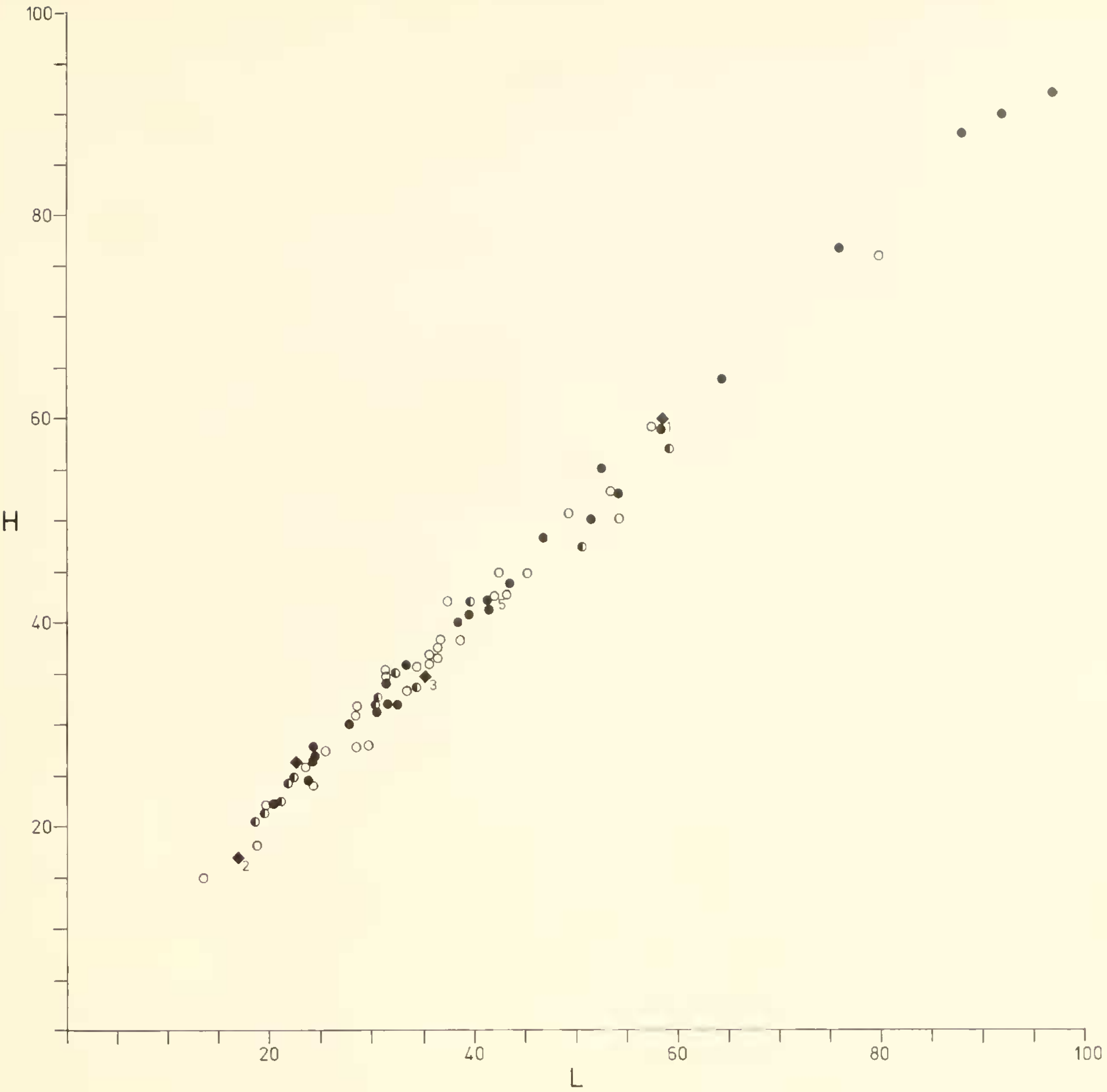
Left valve bearing between 8 and 11 original plicae (text fig. 193), width and height variable both between individuals and in ontogeny. Forms with narrow plicae late in ontogeny adding to number by intercalation (e. g. Pl. 10, Fig. 27). Plicae bearing variably spaced comarginal lamellae; spacing strongly correlated with plical height (e. g. Pl. 10, Fig. 23). Sulci with or without comarginal lamellae; presence strongly correlated with relatively close spacing of plical lamellae (compare Pl. 10, Figs. 28 and 29).

Right valve usually bearing one more plica than left. Closely spaced comarginal striae on both plicae and sulci, sometimes raised into lamellae on the most anterior and posterior of the plicae (Pl. 10, Fig. 26) and on the ventral part of the medial plicae in large specimens. Both valves bearing numerous fine radial striae in the umbonal region.

Shell thickness usually moderate but becoming quite high in large specimens.

4. DISCUSSION

Although the type material of '*pecten*' *Scarburgensis* Young and Bird appears to have been lost, mention in the original description (see Section 1) of 'nine ribs' can leave little doubt that it was representative of the species described in Section 3 rather than the species with which it was compared ('*P.*' *fibrosus* J. Sowerby). Moreover, the type locality, at the foot of Scarborough Castle, is at a horizon (Hackness Rock) at which the former species is common (see Section 7) but at which the latter appears to be absent. Accordingly the species



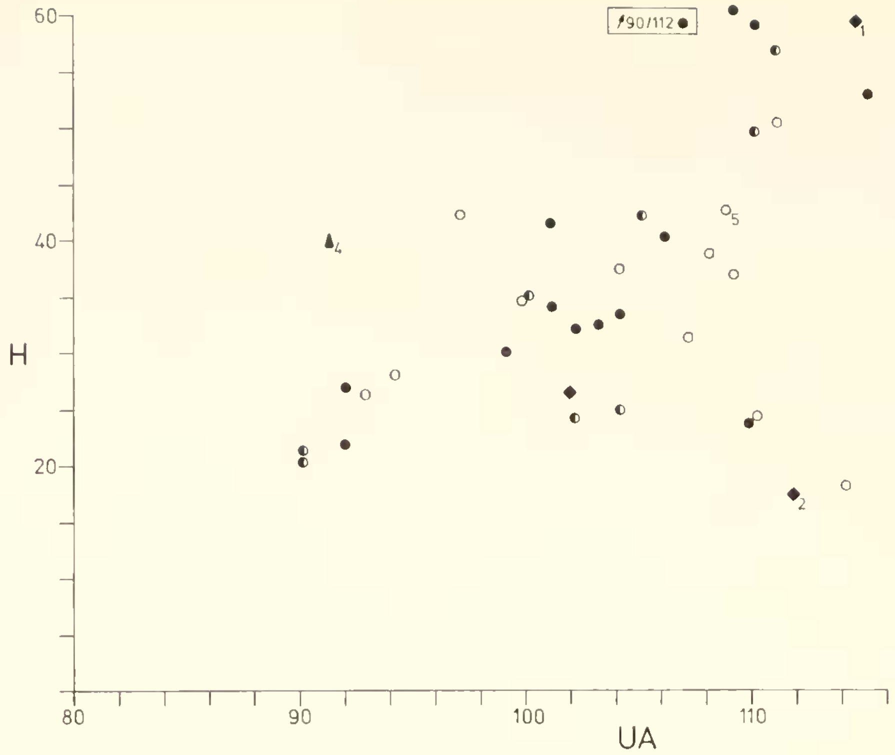
Text fig. 194: *Radulopecten scarburgensis* – height/length.

described in Section 3 is known hereinafter as *Radulopecten scarburgensis.* Duff (1978) has designated as neotype a left valve (SM J12398) whose plicae are initially high and fairly wide but become relatively low and somewhat narrow later in ontogeny, and whose plical lamellae are fairly widely spaced early in ontogeny and closely spaced later, but continuous across the sulci at all stages of growth.

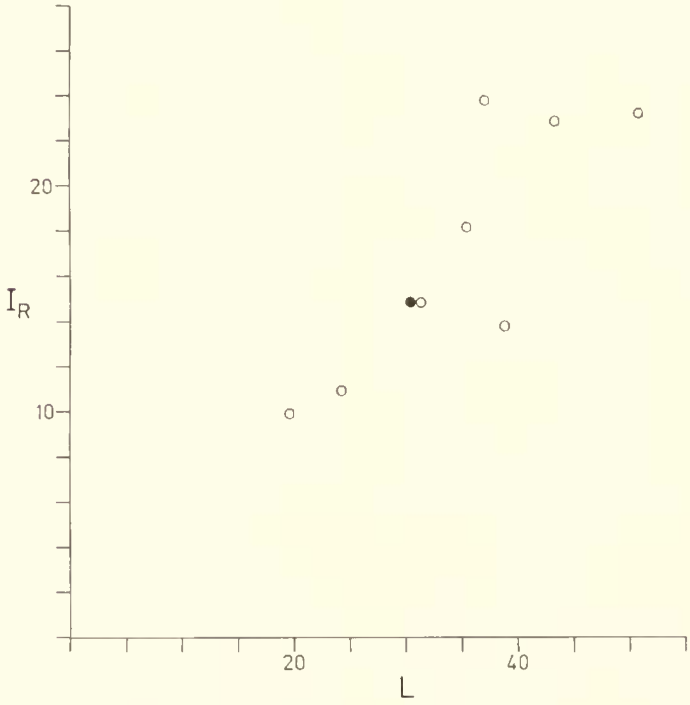
Phillips (1829) and d'Orbigny (1850) misinterpreted J. Sowerby's (1816) hypodigm for '*P.*' *fibrosus* and applied this name to specimens of *R. scarburgensis.* Subsequently, numerous authors have similarly misapplied J. Sowerby's specific name (see *R. fibrosus* for a fuller discussion). Brown (1845) realised Phillips' mistake and erected '*P.*' *discrepans* for the latter's figured specimen. d'Orbigny's species '*P.*' *subfibrosus,* erected for forms which are in fact identical to J. Sowerby's species, was itself misapplied by de Loriol (1901, ?1897, ?1900, ?1904) to specimens of *R. scarburgensis.*

The left valve of the figured syntype of '*P.*' *subarmatus* Münster (BSPHG AS VII 621; Pl. 10, Fig. 29; 1) has high and moderately wide plicae throughout ontogeny and widely spaced plical lamellae which are not continuous across the sulci. Quenstedt (1858) applied Münster's specific name to a specimen (GPIT) which has the conical spines diagnostic of *R. sigmaringensis.* By citing specimens from the Tithonian of S. W. Germany (see Section 5 and p. 217) and including '*P.*' ('*Aequipecten*') *Sigmaringensis* in his synonymy, Staesche (1926) indicates that his concept of '*Ae.*' *subarmatus* included forms which are referable to *R. sigmaringensis* as well as to *R. scarburgensis.*

The sole observed type of '*P.*' *subcancellatus* Münster (BSPHG) is a small left valve (H: 17) with low, narrow plicae and continuous comarginal lamellae. The abnormally small number of plicae (7) and low H/UA (2) may distinguish it from *R. scarburgensis.*



Text fig. 195: *Radulopecten scarburgensis* – height/umbonal angle.

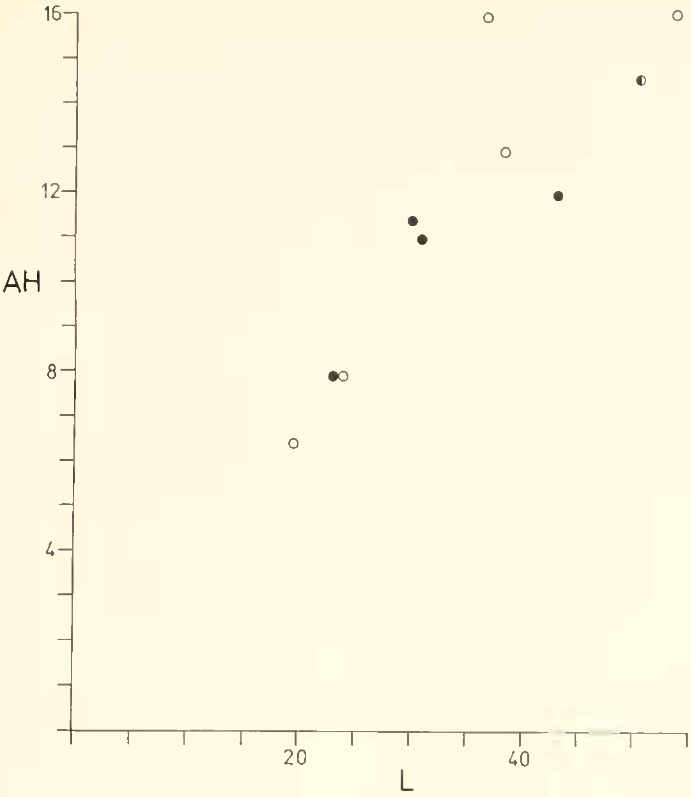


Text fig. 196: *Radulopecten scarburgensis* – intersinal distance on right valve/length.

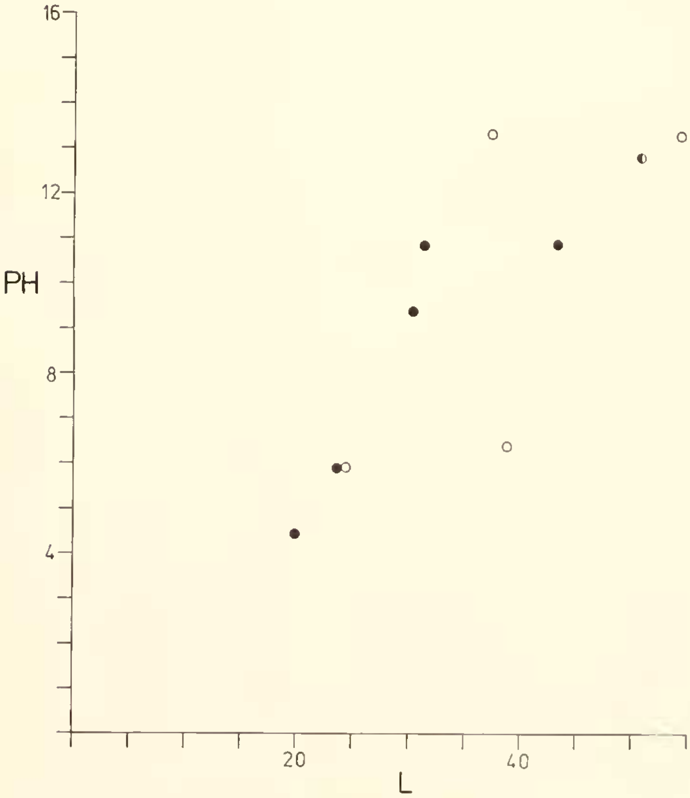
The figures of '*P.*' *Bavoux* CONTEJEAN (3) and '*P.*' *Laurae* ÉTALLON depict specimens with narrow original plicae and numerous intercalaries.

'*P.*' ('*Ae.*') *Catharinae* ROLLIER was said to be between '*P.*' *Laurae* and '*P.*' *subarmatus* and therefore cannot be accorded a specific distinction in the light of the preceding discussion. '*P.*' ('*Ae.*') sp. nov; ROLLIER was said to be a 'mutation' of '*P.*' *Laurae*. The figured specimen is too poorly preserved for specific determination.

'*Chlamys*' (*R.*) *tipperi* COX and '*Ch.*' (*R.*) *moondanensis* COX were both compared to '*P.*' *Laurae*. The former comes from an anomalously early horizon (Bajocian) for *R. scarburgensis* and the paratype (BM L63157) has an unusually high H/UA (4). The latter comes from an abnormally late



Text fig. 197: *Radulopecten scarburgensis* – anterior hinge length/length.



Text fig. 198: *Radulopecten scarburgensis* – posterior hinge length/length.

horizon (Tithonian) and the paratype (BM L75243; Pl. 11, Fig. 1), a right valve, has rather widely spaced comarginal ornament. This could, however, be due to its exceptional size (H: ≃170). '*Ch.*' *(R.) kinjeleensis* Cox was compared to '*Ch.*' *(R.) inaequicostata* (= *R. inequicostatus* herein) but the presence of 10 plicae allies it with *R. scarburgensis* although the byssal notch is unusually deep for the latter species.

The original description of '*P.*' *subinaequicostatus* Kasansky has proved impossible to trace but Borissiak and Ivanoff's (1917) specimen figured under this name (5) has 9 plicae and is indistinguishable from *R. scarburgensis*.

Newton's (1921) figure of '*Ch.*' *articulatus* (Schlotheim) is much closer to *R. scarburgensis* than to Schlotheim's species (? = *R. inequicostatus*).

5. STRATIGRAPHIC RANGE

With the exception of a doubtful occurrence in the Bajocian of Iran (Cox, 1936; see Section 4) there are no records of *R. scarburgensis* until the L. Callovian when a few specimens are known from the Kellaways Rock (Calloviense zone) of Yorkshire (BM 11030, YM 605e) and Wiltshire (Duff, 1978) and from the L. Oxford Clay (Calloviense zone) of Bedfordshire (Duff, 1978). A specimen from the U. Cornbrash (Macrocephalus zone) of Yorkshire (BM 47431; Pl. 10, Fig. 19) may be a slightly earlier representative of *R. scarburgensis* but the possibility cannot be excluded that it is an extreme variant of *R. fibrosus*. All remaining substage-defined records of *R. scarburgensis* in the Callovian are from the U. Callovian, where the species is locally common (see Section 7).

The species is locally common throughout the Oxfordian but undoubted Kimmeridgian records are limited to three specimens from S. W. Germany (GPIT, BSPHG [2]), and a few from the Jura (Contejean, 1859; de Loriol, 1878, 1881). Stefanini (1939) records an indeterminate number of specimens from the Oxfordian/Kimmeridgian of Somalia and Dietrich (1933) records a single specimen from the 'Kimmeridgian/Portlandian' of Tanzania.

The species may occur in the Tithonian of Cutch, N. W. India (Cox, 1952; see Section 4).

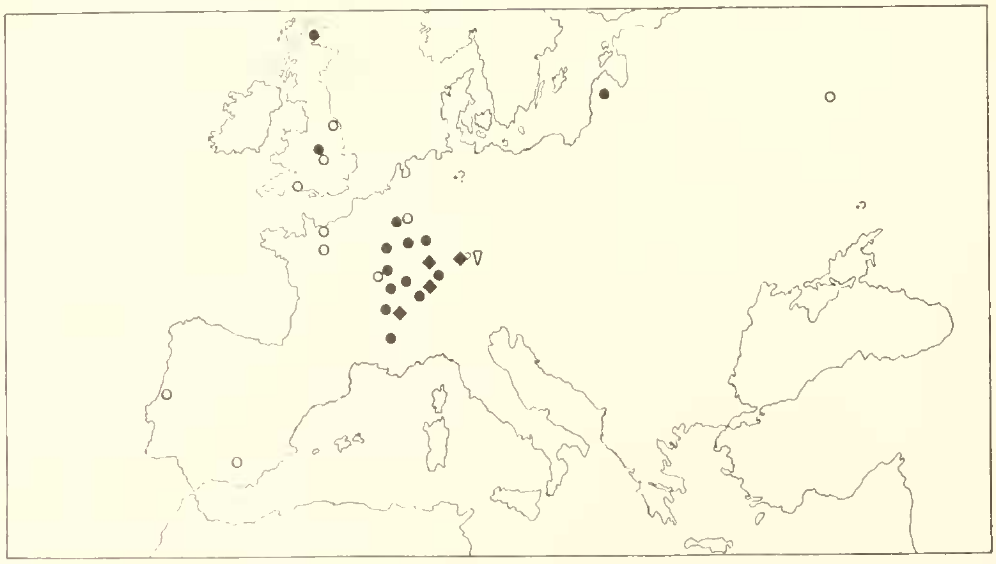
6. GEOGRAPHIC RANGE

In the Callovian and Oxfordian *R. scarburgensis* was a widespread species in Europe (text fig. 199) and extended along the southern margin of Tethys at least as far as the equator (text fig. 200). Within this region local distribution was largely related to the development of argillaceous facies (see Section 8). The absence of the species from such facies in the Kimmeridgian of N. W. Europe is roughly correlated with its first occurrence at the southerly palaeolatitude of Tanzania (see Section 5) and seems to imply a wholesale southward migration.

7. DESCRIPTION OF ECOLOGY

R. scarburgensis occurs commonly in clays of the Lamberti zone (U. Callovian) in Buckinghamshire (J. Hudson and Palframan, 1969) in association with a benthic fauna dominated by *Pinna* and *Gryphaea*. The maximum height attained is 50 mm (OUM J9548). The species is also quite common in roughly contemporaneous chamosite oolith-bearing sandstones in Yorkshire (Hackness Rock). Young and Bird (1822) cite specimens 3" (76 mm) long from this horizon although the largest known museum specimen (Duff, 1978) has a length of only 41.5 mm (H: ≃48).

In France, *R. scarburgensis* is quite common in the U. Callovian clays of the Dijon area (DM) where a maximum height of 55 mm is attained. Numerous 'Callovian' museum specimens (MNO) from Normandy and Sarthe are almost certainly derived from similar facies and may well be contemporaneous. The maximum height is 76 mm. Although not common *R. scarburgensis* also occurs in argillaceous facies in the U. Callovian of Dorset (BM unnumbered), E. Spain (Behmel, 1970), central Russia (Borissiak and Ivanoff, 1917) and S. Israel (R. Hudson, 1958). Other Callovian records are limited to two specimens (BM LL30877-8) from muddy sandstones in Portugal, an indeterminate number of specimens,


Text fig. 199: *Radulopecten scarburgensis* – European distribution.

Text fig. 200: *Radulopecten scarburgensis* – World distribution (Callovian reconstruction).

probably from similar facies, in the Caucasus (Borissiak and Ivanoff, 1917) and the few specimens from the lowest substage mentioned in Section 5.

The great majority of Callovian examples of *R. scarburgensis* have initially high original plicae which subsequently undergo an allometric reduction in height such that the comarginal lamellae on the left valve, after being widely spaced early in ontogeny, become relatively closely spaced. The original plicae are usually fairly wide throughout ontogeny so that development of intercalary plicae is not common. Pl. 10, Fig. 28 illustrates a typical specimen.

In the L. Oxfordian *R. scarburgensis* occurs quite commonly in the 'Terrain à Chailles' of Alsace (Roeder, 1882) and the Yonne (Peron, 1905). The species also occurs commonly in the marls and marly limestones of the 'Oxfordien Supérieur et Moyen' of the Ledonian Jura (de Loriol, 1904) and in similar facies at an unspecified horizon in the Oxfordian of Sinai (Douvillé, 1916). Museum specimens (NM) from the coral-rich U. Oxfordian sediments of Meurthe and Moselle are fairly common and reach a maximum height of 90 mm. Museum specimens (MNP) from similar facies in the U. Oxfordian of the Yonne are also not uncommon and reach a maximum height of 92 mm. *R. scarburgensis* does not appear to be common elsewhere in the Oxfordian. Specimens from the coral-rich L. Oxfordian of the Bernese Jura (de Loriol, 1894), from coralliferous limestones and marls in the U. Oxfordian of the Rhone (Lissajous, 1910; Roman, 1926) and from clays of the L. Oxfordian in central England (BM LL7546) constitute the only other records where facies are known.

A high proportion of Oxfordian specimens of *R. scarburgensis* have initially low plicae but plical height usually increases isometrically (e. g. Pl. 10, Fig. 27) as it also does in specimens with initially high plicae. Consequently forms with initially widely spaced and forms with initially closely spaced comarginal lamellae are both well represented but forms with closely spaced lamellae late in ontogeny are quite rare. A fairly high proportion of specimens have narrow original plicae late in ontogeny so development of intercalary plicae is quite frequent (e. g. Pl. 10, Fig. 27).

All of the relatively few European Kimmeridgian records (see Section 5) excepting Contejean's (1859) single specimen (from coral/*Diceras* facies) are derived from argillaceous sediments. The pattern of ornamental variation is much the same as in the Oxfordian except that forms whose plicae undergo an allometric reduction in height (and which consequently have closely spaced lamellae late in ontogeny) are apparently absent. Pl. 10, Fig. 29 illustrates a Kimmeridgian specimen.

8. INTERPRETATION OF ECOLOGY

It is clear from Section 7 that the low energy environment of argillaceous sedimentation was favourable for *R. scarburgensis*. The species could not, however, tolerate low energy conditions where accompanied by reduced oxygen tension (e. g. L. Oxford Clay of England).

The isolated occurrence of numerous specimens of *R. scarburgensis* in arenaceous sediments in the U. Callovian of Yorkshire indicates that high energy environments could be tolerated and this seems to be emphasised by the fairly common occurrence and large size of specimens in the coral-rich U. Oxfordian of the Yonne and Meurthe and Moselle. In the latter cases, however, the micritic matrix of museum specimens suggests that the species may have colonised low energy inter-reef lime muds.

Chlamys septemradiata, a Recent free-living species which inhabits deep water muds in the First of Clyde (J. Allen, 1953), is a close morphological analogue of *R. scarburgensis*.

9. FUNCTIONAL MORPHOLOGY

The small byssal notch and equal auricles of most specimens of *R. scarburgensis* imply abandonment of byssal fixation in favour of reclining at an early age. Even in forms with a moderately deep byssal notch it is very doubtful whether attachment was maintained to heights anywhere near the maximum. All examples of the Recent analogue *Ch. septemradiata* observed by the author, including specimens as small as H: 30, were free living.

Ontogenetic increase in umbonal angle is paradigmatic for prolonging swimming ability, presumably as a means of escaping predators. Shell thickening in large specimens is non-paradigmatic but may represent a switch to a 'siege' policy towards predators late in life.

The lack of comarginal lamellae on the medial plicae of the right valve at all but the latest ontogenetic stages could be due to inhibited growth through contact with the substrate (Staesche, 1926) but is more probably due to swimming activity (see above) leading to abrasion.

10. ORIGINS AND EVOLUTION

The most likely ancestor for *R. scarburgensis* is *R. vagans*. The important changes in morphology, the early development and relatively invariant number of initial plicae, could have been brought about by heterochronic acceleration and 'genetic assimilation' (Waddington, 1957) so modifications of the regulatory system may underlie the greater part of trans-specific evolution.

There is no reason to suppose that the stratigraphic change in the mean form of the ornament of *R. scarburgensis* (see Section 7) is anything other than an evolutionary phenomenon. Since there appears to be no addition to the range of ornamental variation the change in mean form could have resulted purely from selection (i. e. without addition to the gene pool). The reason for this phyletic evolution is not apparent.

The maximum height of available museum specimens increases from the Callovian (76 mm) to the Oxfordian (92 mm). The Kimmeridgian value (59 mm; BSPHG AS VII 621) is derived from a very small sample (see Section 5) and therefore does not necessarily imply reversal of a phyletic trend towards greater size. Possibly conspecific specimens from the Tithonian (see Section 4) have a maximum height of 170 mm.

Although the Kimmeridgian decline of *R. scarburgensis* is contemporaneous with the first records of *R. sigmaringensis* there is no reason to suppose that the former was outcompeted by the latter as *R. sigmaringensis* is a very rare species in the Kimmeridgian.

Radulopecten sigmaringensis (Rollier 1915)

Pl. 11, Figs. 5, 6; text figs. 201, 202

Synonymy

v 1858	*Pecten subarmatus* Münster; Quenstedt, p. 754, pl. 72, figs. 8, 9 (non Münster sp.).
v* 1915	*Pecten (Aequipecten) Sigmaringensis* sp. nov; Rollier, p. 474.
p 1926	*Aequipecten subarmatus* (Münster); Staesche, p. 68 (non Münster sp.).

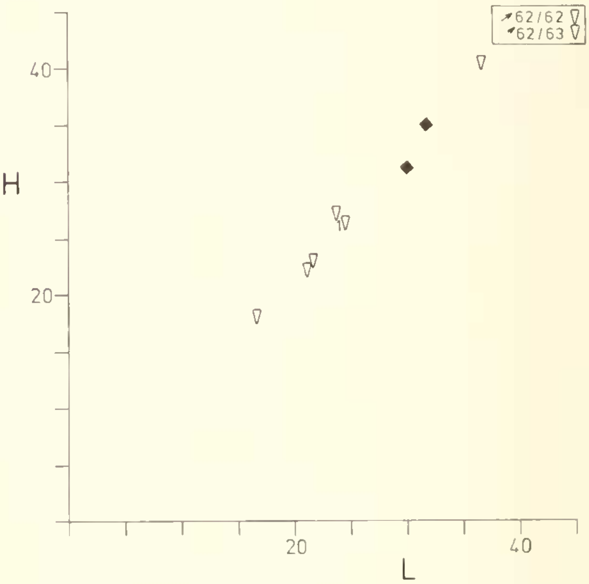
Holotype (M) of *Pecten (Aequipecten) Sigmaringensis* Rollier 1915, p. 474; GPIT 4-72-8; figured Quenstedt, 1858, pl. 72, figs. 8, 9; Pl. 11, Fig. 6 herein; H: 27.5, L: 24, HAA: 5.5, AH: 7, PH: 7, I_R: 13, N: 1, PL: 12, UA: 92; Malm ζ (L./M. Tithonian), Jungnau, S. W. Germany.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

'Le '*P.*' *subarmatus* figuré par Quenstedt, Jura (1858), p. 754, 758, t. 92, f. 8–9, du Danubien infér. (W. Jura ζ) des environs de Sigmaringen (Hohrain) ne répond plus du tout à l'espece du Crussolien, elle est beaucoup plus aigü (angle apical 88°) sans costules intermédiaires, et portant des écailles coniques, pointues. Je propose de l'appeler *P. (Ae.) Sigmaringensis* sp. nov. i. f. Qu. *P. subarmatus*, non Goldf.'

2. AMENDED DIAGNOSIS

Distinguished from all other species of *Radulopecten* by the spinose rather than lamellose ornament on the plicae.



Text fig. 201: *Radulopecten sigmaringensis* – height/length.

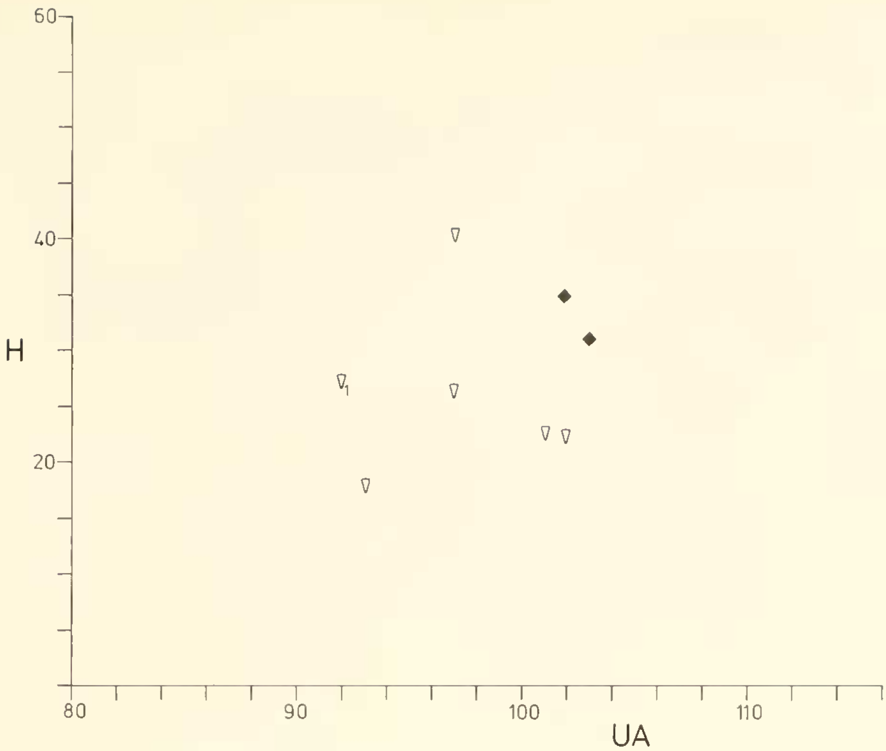
3. AMENDED DESCRIPTION

Essentially very similar to *R. scarburgensis*, differing only by the diagnostic feature (see Section 2; Pl. 11, Fig. 5), by the invariant number of original plicae (LV: 11, RV: 12), by the rarity of intercalary plicae and by the smaller maximum size (L_{max}: 68; GPIT). H/L and H/UA are plotted in text figs. 201, 202.

4. DISCUSSION

A number of examples of the species described in Section 3 in the GPIT are wrongly labelled *Pecten subarmatus* Münster (= *Radulopecten scarburgensis*), including the specimen (Pl. 11, Fig. 6; 1) figured by Quenstedt (1858). The latter formed the basis for '*P.*' ('*Aequipecten*') *Sigmaringensis* Rollier and becomes ipso facto the holotype (M).

Staesche's (1926) record of '*Ae.*' *subarmatus* is discussed under *R. scarburgensis*.



Text fig. 202: *Radulopecten sigmaringensis* – height/umbonal angle.

5. STRATIGRAPHIC RANGE

Three specimens (GPIT) from the Malm ε (Kimmeridgian) constitute the earliest records of *R. sigmaringensis*. All other records are from the Malm ζ (L./M. Tithonian) apart from a single specimen (MNS) from the 'Portlandian' (U. Tithonian).

6. GEOGRAPHIC RANGE

All records of *R. sigmaringensis* are from S. W. Germany except for the single U. Tithonian specimen which is from Nantua (French Jura).

7. DESCRIPTION OF ECOLOGY

Four of the twelve 'Malm ζ' specimens (GPIT[11], BM; see Section 5) are also labelled 'Zementmergel' and by the similarity of the matrix it seems probable that the remaining specimens are likewise derived from this formation, a L. Tithonian marl sequence.

Specimens from the Kimmeridgian and U. Tithonian are derived from marly limestones.

8. INTERPRETATION OF ECOLOGY

The fine-grained sediments in which *R. sigmaringensis* is found probably afforded a soft substrate at the time of deposition.

9. FUNCTIONAL MORPHOLOGY

Since *R. sigmaringensis* is morphologically almost identical to *R. scarburgensis* a similar reclining mode of life after a brief byssate phase can be inferred.

The function, if any, of the plical spines of *R. sigmaringensis* is, like the plical lamellae of *R. scarburgensis*, unclear.

The fuller development on the left valve and small size of both spines and lamellae rules out any possibility that they might represent a 'snow-shoe' adaptation to the soft substrates occupied by *R. sigmaringensis* and *R. scarburgensis*.

10. ORIGINS AND EVOLUTION

R. sigmaringensis almost certainly arose from *R. scarburgensis* and since the former species is first known within the geographic range of the latter the possibility of sympatric speciation cannot be ruled out. The development of spines rather than lamellae cannot be explained by heterochrony so trans-specific evolution probably involved some change in the structural genome.

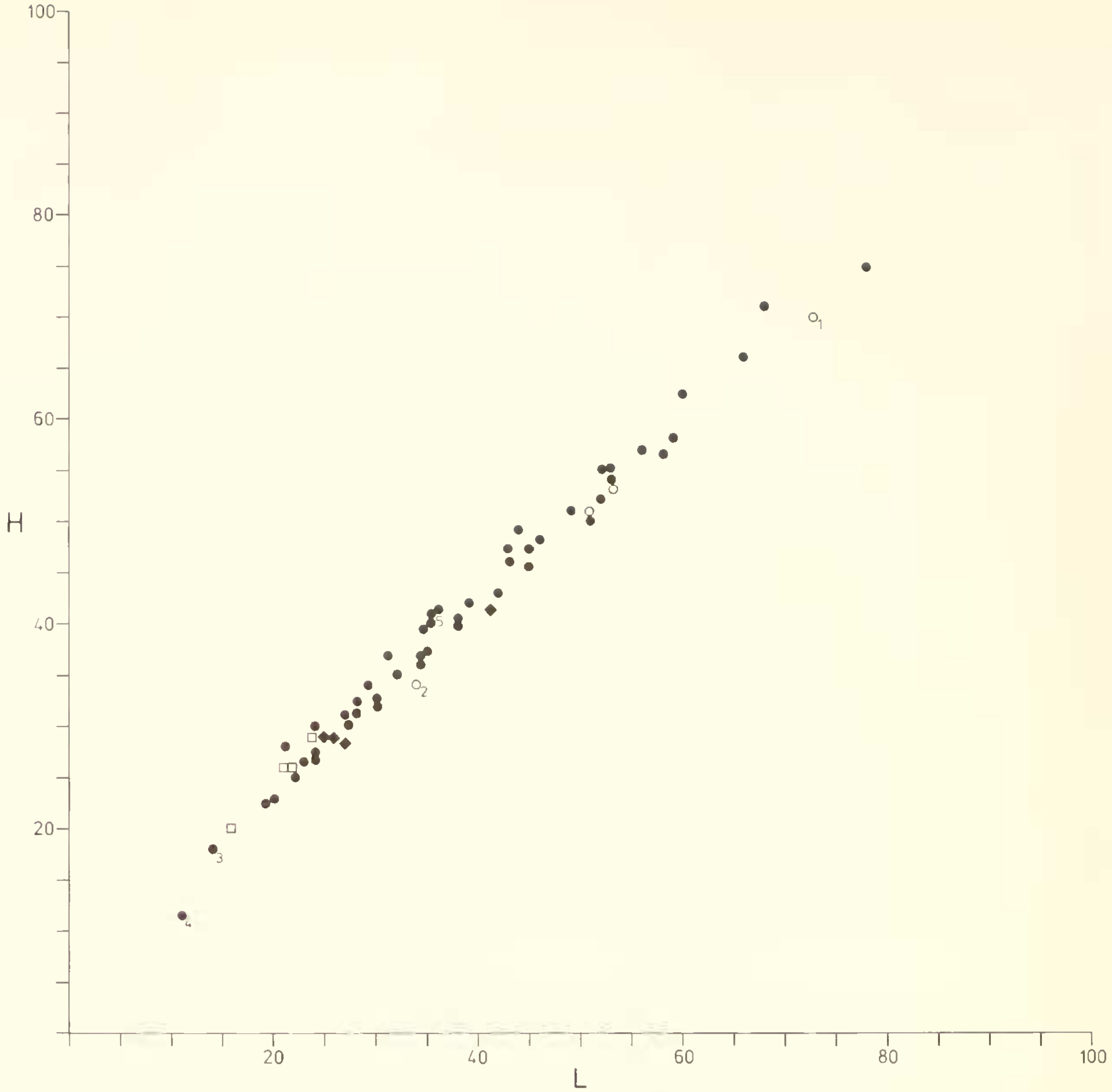
The few available specimens (16) give no indication of any phyletic trends in *R. sigmaringensis*. The largest specimen (L: 68; GPIT) is from the L. Tithonian.

Radulopecten inequicostatus (Young and Bird 1822)

Pl. 11, Figs. 2, 4, 7–9; text figs. 203–213

Synonymy

? 1820	*Pectinites articulatus* sp. nov; Schlotheim, p. 227.
1822	*Pecten inequicostatus* sp. nov; Young and Bird, p. 235, pl. 9, fig. 7.
1829	*Pecten inaequicostata* sp. nov; Phillips, p. 129, pl. 4, fig. 40.
v non 1833	*Pecten articulatus* (Schlotheim); Goldfuss, p. 47, pl. 90, fig. 10.
1836	*Pecten octocostatus* sp. nov; Roemer, p. 69, pl. 3, fig. 18.



Text fig. 203: *Radulopecten inequicostatus* – height/length.

1839 *Pecten septemcostatus* sp. nov; Roemer, p. 212.

? *1839* *Pecten inaequicostata* Phillips; Bean, p. 60.

v*1850 *Pecten corallinus* sp. nov; d'Orbigny, v. 2, p. 22 (Boule, 1929, v. 18, p. 172, pl. 19, fig. 18).

? 1852 *Pecten biplex* sp. nov; Buvignier, p. 23, pl. 19, figs. 1–6.

non 1853 *Pecten articulatus* (Schlotheim); Morris and Lycett, p. 32, pl. 33, fig. 12.

non 1853 *Pecten articulatus* (Schlotheim); Chapuis and Dewalque, p. 212, pl. 29, fig. 3.

v non 1858 *Pecten articulatus* (Schlotheim); Quenstedt, p. 754, pl. 92, fig. 11.

1860 *Pecten corallinus* d'Orbigny; Coquand, p. 79.

1862 *Pecten octocostatus* Roemer; Thurmann and Étallon, p. 252, pl. 35, fig. 7.

non 1862 *Pecten articulatus* (Schlotheim); Thurmann and Étallon, p. 255, pl. 36, fig. 2.

? 1862 *Pecten semiplicatus* sp. nov; Thurmann and Étallon, p. 261, pl. 36, fig. 17.

1863 *Pecten inaequicostatus* Phillips; Lycett, p. 32, pl. 33, fig. 1 (non fig. 1a).

1864 *Pecten inaequicostatus* Phillips; v. Seebach, p. 97.

1866 *Pecten inaequicostatus* Phillips; Oppel, p. 290.

1872 *Pecten inaequicostatus* Phillips; de Loriol et al., p. 388.

1881 *Pecten inaequicostatus* Phillips; de Loriol, p. 87, pl. 12.

? 1883 *Pecten inaequicostatus* Phillips; Lahusen, p. 22, pl. 1, figs. 15, 16.

1893 *Chlamys (Pecten) inaequicostata* (Phillips); Siemiradzki, p. 118.

1893 *Pecten inaequicostatus* Phillips; de Loriol, p. 301, pl. 32, figs. 13–15.

1893 *Pecten Ursannensis* sp. nov; de Loriol, p. 311, pl. 33, figs. 5–7.

1894 *Pecten inaequicostatus* Phillips; de Loriol, p. 44.

1895 *Pecten Neckeri* sp. nov; de Loriol, p. 43, pl. 10, fig. 5.

? 1896 *Pecten inaequicostatus* Phillips; Semenow, p. 63.

non 1898 *Pecten articulatus* (Schlotheim); Greppin, p. 128.

v 1905 *Pecten inaequicostatus* Phillips; Peron, p. 218.

? *1905* *Pecten (Aequipecten) octocostatus* Roemer; Kilian and Guébhard, p. 766.

? *1905* *Pecten (Aequipecten)* cf. *inaequicostatus* Phillips; Kilian and Guébhard, p. 805.

? 1915 *Pecten* sp. (*inaequicostatus* Phillips?); Krenkel, p. 297.

? 1915 *Pecten* sp. (sp. nova?); Krenkel, p. 298.

v* non 1916 *Chlamys articulata* var. *notgroviensis* var. nov; Paris and Richardson, p. 525, pl. 45, fig. 2.

v* non 1916 *Chlamys articulata* var. *sauzeana* var. nov; Paris and Richardson, p. 526, pl. 45, figs. 3a, 3b.

non 1920 *Pecten articulatus* (Schlotheim); Faure-Marguerit, p. 59.

non 1920 *Pecten articulatus* (Schlotheim) var. passant à *Pecten anastomoplicus* Gemmellaro and Di Blasi; Faure-Marguerit, p. 59.

? *1925* *Pecten* cf. *inaequicostatus* Phillips; Read et al., p. 81.

1926 *Chlamys inaequicostata* (Phillips); Roman, p. 194.

v 1926 *Aequipecten inaequicostatus* (Phillips); Arkell, p. 545, pl. 34, fig. 1.

v 1931a *Chlamys (Radulopecten) inaequicostatus* (Phillips); Arkell, p. 118, (1930a) pl. 8, figs. 4–7.

1935a *Chlamys inequicostata* (Young and Bird); Arkell, p. xiv.

1935a *Chlamys (Aequipecten)* sp; Cox, p. 177, pl. 23, fig. 8.

1936a *Chlamys (Radulopecten) inequicostata* (Young and Bird); Arkell, pl. 52, figs. 1, 3.

? 1936 *Aequipecten biplex* (Buvignier); Dechaseaux, p. 150.

1936 *Aequipecten inaequicostatus* (Phillips); Dechaseaux, p. 51, pl. 7, fig. 6.

1936 *Aequipecten ursannensis* (de Loriol); Dechaseaux, p. 57, pl. 8, fig. 7.

? 1936 *Aequipecten semiplicatus* (Étallon); Dechaseaux, p. 58.

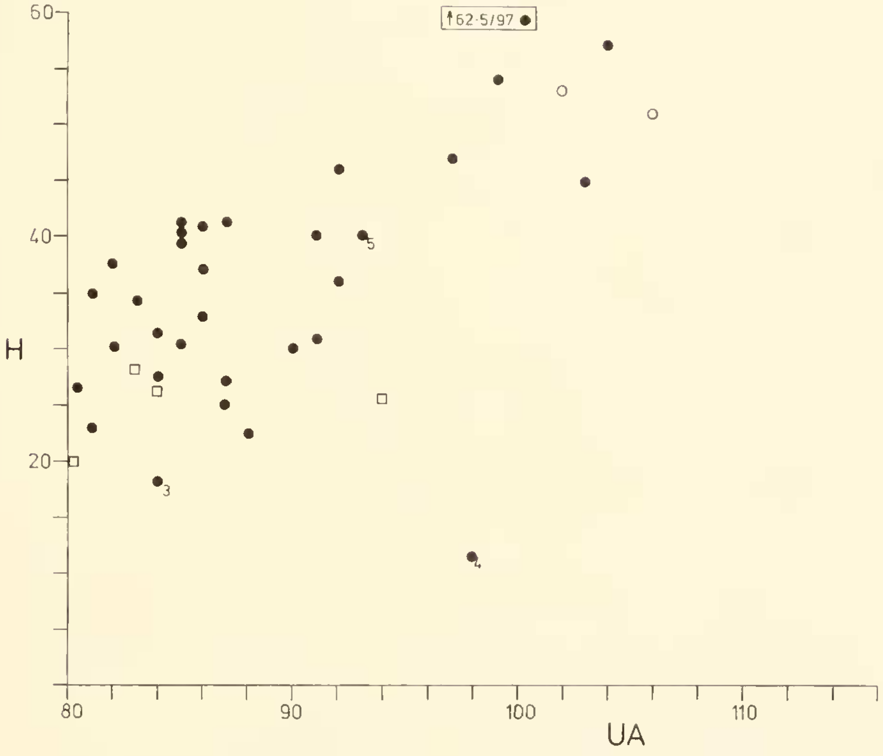
1958 *Chlamys (Radulopecten)* cf. *inaequicostata* (Phillips); R. Hudson, p. 423.

? 1959 *Chlamys (Radulopecten) nagatakensis* Kurata and Kimura; Tamura, p. 58, pl. 6, figs. 31, 32.

1965 *Chlamys (Radulopecten) inaequicostata* (Phillips); Cox, p. 59, pl. 7, fig. 6.

1971 *Chlamys (Radulopecten) inaequicostata* (Phillips); Worssam and Ivimey-Cook, p. 40.

Neotype of *Pecten inequicostatus* Young and Bird 1822, p. 235, pl. 9, fig. 7 designated herein; BM 23173; Pl. 11, Fig. 8 herein; Corallian (Oxfordian), Malton, Yorkshire.



Text fig. 204: *Radulopecten inequicostatus* – height/umbonal angle.

1. ORIGINAL DIAGNOSIS AND DESCRIPTION

'Nos. 2 and 7 are of that class of pectens which have a crooked appearance, leaning or bending to one side...

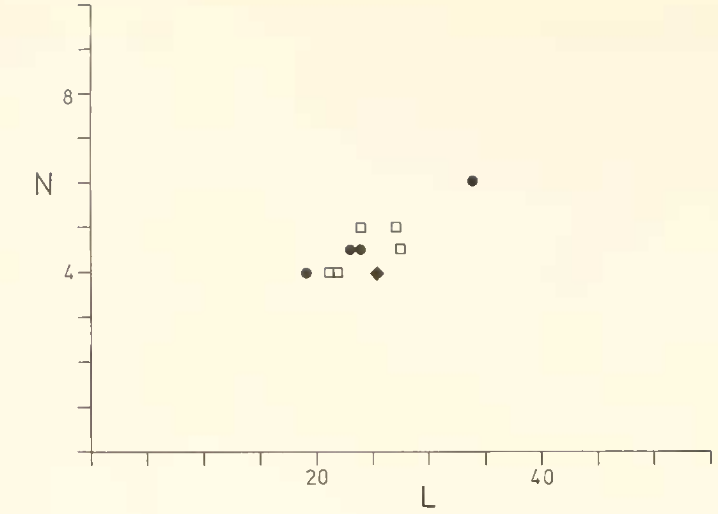
No. 7, similar in shape [to '*p.*' *Roseburiensis* and '*p.*' *plagiostomus*], is from the oolite. It has seven or eight ribs, of which those in the middle are vastly larger than those on either side. If it is not the *p. flavicans*, we might name it *p. inequicostatus*.

2. AMENDED DIAGNOSIS

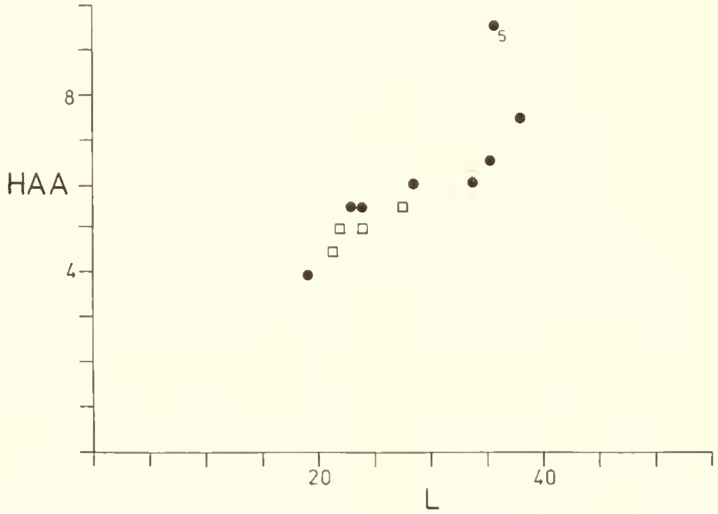
Distinguished from all other species of *Radulopecten* by the inequality of the initial plicae.

3. AMENDED DESCRIPTION

Essentially very similar to *R. vagans*. Differing by the diagnostic feature (see Section 2); by the consistently early



Text fig. 205: *Radulopecten inequicostatus* – depth of byssal notch/length.



Text fig. 206: *Radulopecten inequicostatus* – height of anterior auricle/length.

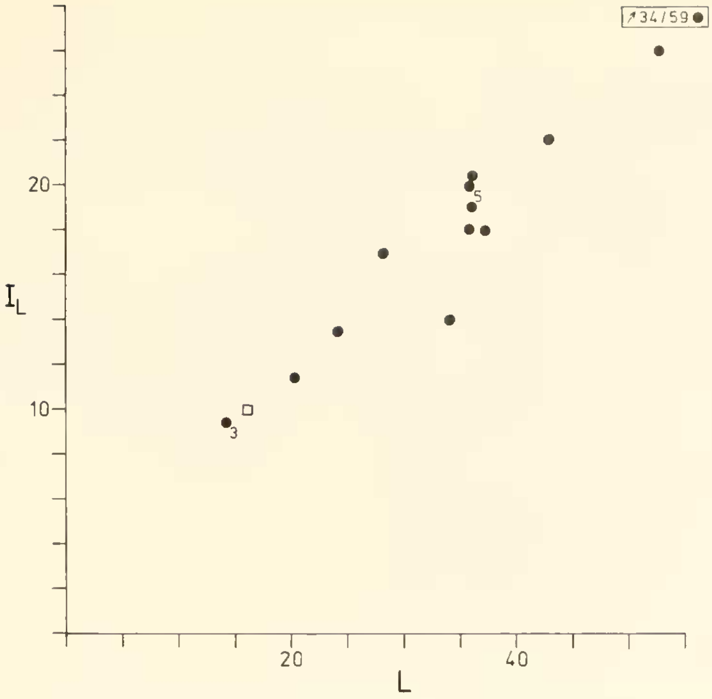
development of plicae, relatively invariant number of initial plicae (5–9; text fig. 211) and rarity of intercalary plicae; by the consistently wide spacing of the plical lamellae on the left valve and lack of lamellae on the right valve, even in large specimens (Pl. 11, Fig. 9); by the greater convexity, thicker shell (Pl. 11, Fig. 4) and more common attainment of a large size (see Section 7; H_{max}: 75; MNP); by the ontogenetic decrease in H/L (text fig. 203) and by the marked ontogenetic increase in umbonal angle and larger mean H/UA (text fig. 204). Other metric proportions are plotted in text figs. 205–210.

Although the plicae are of unequal size in any individual the pattern of variation is relatively consistent between individuals, with the medial and antero-medial plicae usually the widest.

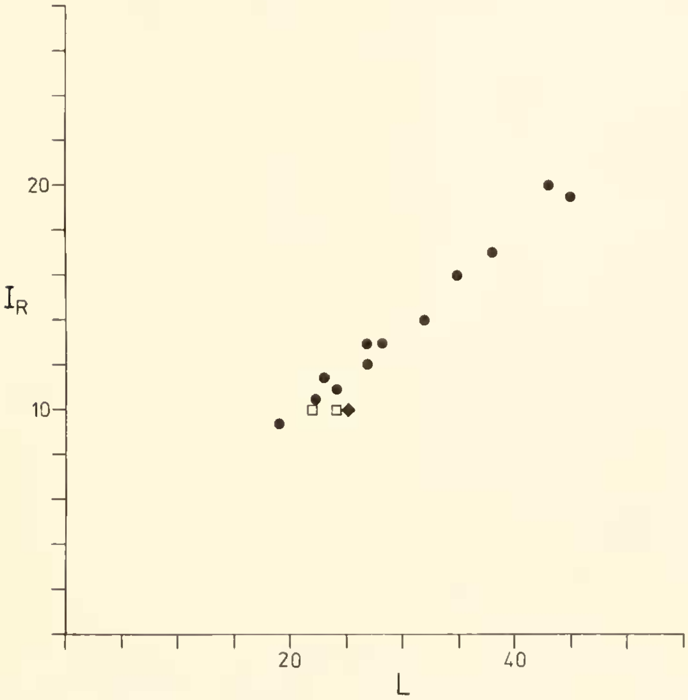
4. DISCUSSION

Most authors have applied PHILLIPS (1829) name *inaequicostatus* to the species described in Section 3. However, ARKELL (1935a) pointed out that YOUNG and BIRD (1822) described and figured an undoubted example of the species described in Section 3 under *'pecten' inequicostatus* and that this name should therefore be the senior synonym. YOUNG and BIRD's specimen is without doubt lost so a neotype (BM 23173; Pl. 11, Fig. 8) is herein designated.

A figured specimen assigned to *'P.' inaequicostatus* PHILLIPS by LAHUSEN (1883) is derived from an unusually early horizon (Callovian; see Section 5) and has 12 plicae and abnormally low values of HAA/L and N/L (1). It more probably belongs to *Radulopecten scarburgensis.* In view of the possibility of confusion for *R. scarburgensis* unfigured Callovian specimens either assigned to (BEAN, 1839; LYCETT, 1863; SEMENOW, 1896) or compared with (KRENKEL, 1915; READ et al., 1925) PHILLIPS's species can only be tentatively accepted as representatives of *R. inequicostatus.* LYCETT's (1863) misuse of PHILLIPS's specific name for a L. Callovian specimen of *R. vagans* is discussed under the latter species. KILIAN and GUÉBHARD's (1905) record of *'P.' ('Aequipecten')* cf. *inaequicostatus* from the 'U. Kimmeridgian – L. Portlandian' can only be tentatively synonymised in view of the exceptionally late stratigraphic horizon and lack of a figure.



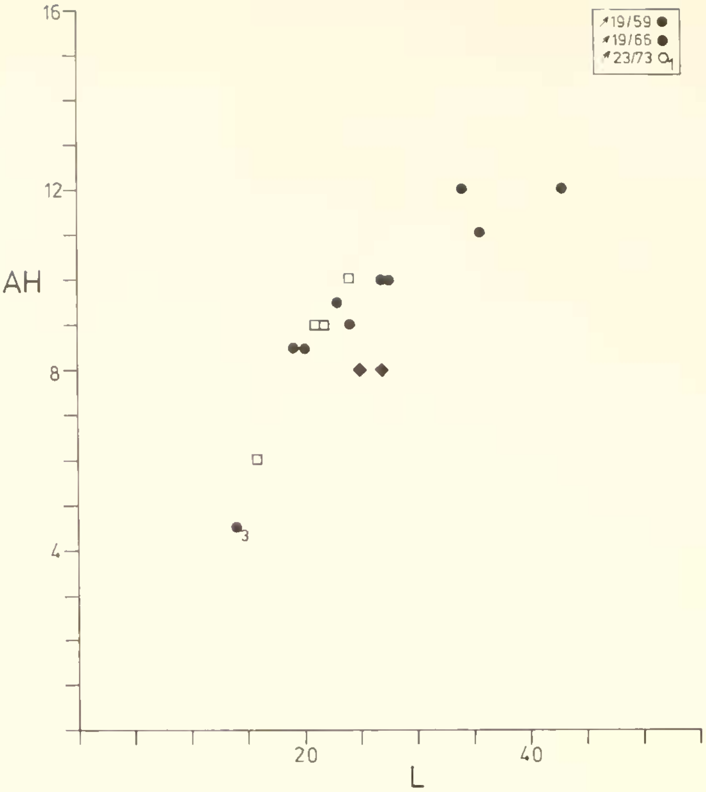
Text fig. 207: *Radulopecten inequicostatus* – intersinal distance on left valve/length.



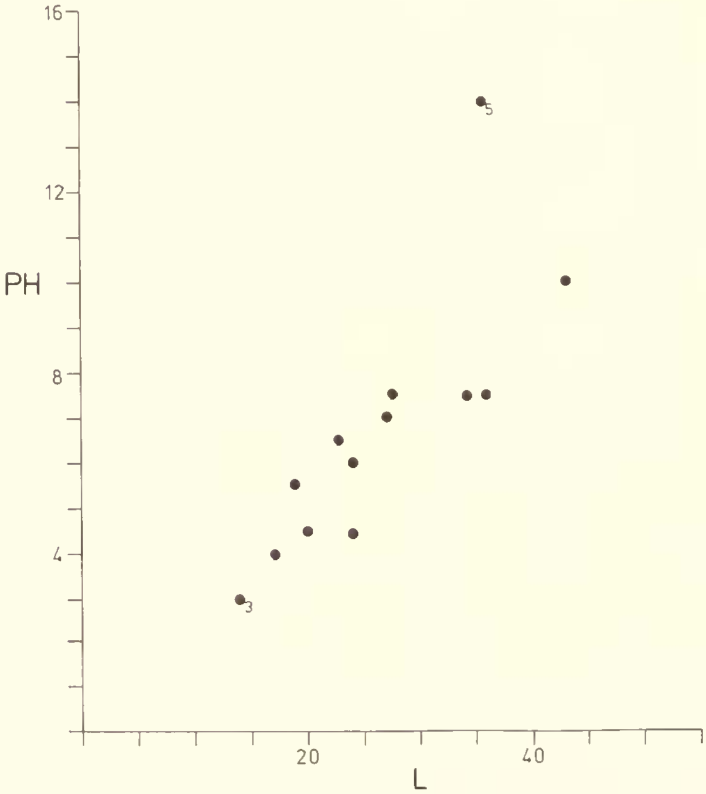
Text fig. 208: *Radulopecten inequicostatus* – intersinal distance on right valve/length.

The figure of *'P.' biplex* Buvignier (2) depicts a specimen which is in many respects similar to *R. inequicostatus* but which appears to possess the intercalary plicae more characteristic of *R. vagans*. Dechaseaux (1936), who may have had access to the specimen, has allied Buvignier's species with *'Aequipecten' inaequicostatus* (Phillips). The latter author allied Étallon's species *'P.' semiplicatus* with *'Ae.' vagans* but the original description specifies its closeness to Roemer's (1836) species *'P.' octocostatus* (emend. *septemcostatus* 1839), an undoubted synonym of *R. inequicostatus*. Kilian and Guébhard's (1905) unillustrated record of *'P.' ('Ae.') octocostatus* from the Callovian can only be tentatively synonymised owing to the possibility of confusion for *R. scarburgensis* (see above).

The figures of *'P.' Neckeri* de Loriol and *'P.' Ursannensis* de Loriol both depict specimens with 6 plicae and metric proportions of the former (3) are indistinguishable from *R. inequicostatus*. H/UA of the latter (4) is abnormally low



Text fig. 209: *Radulopecten inequicostatus* – anterior hinge length/length.



Text fig. 210: *Radulopecten inequicostatus* – posterior hinge length/length.

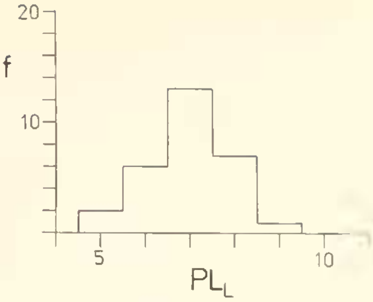
but this could be due to inaccurate drawing and is no basis for a specific separation.

The ornament of the remaining syntypes of *'P.' corallinus* D'ORBIGNY (MNO 4290, 4290B) is indistinguishable from *R. inequicostatus*. The exceptionally high HAA/L and PH/L (5) of MNO 4290 is herein considered to represent extreme variation within *R. inequicostatus*.

The author has been unable to trace the original description of *'Chlamys' (R.) nagatakensis* KURATA and KIMURA. TAMURA's (1959) use of the name is for a specimen from Japan said to differ from *'Ch.' (R.) inaequicostata* (PHILLIPS) only by the presence of striae on the plicae. Since this is in fact a feature of well preserved examples of PHILLIPS's species (= *R. inequicostatus)* TAMURA's specimen may well be conspecific and KURATA and KIMURA's species synonymous with *R. inequicostatus*.

COX (1935a) compared a specimen from Somalia with PHILLIPS' species. The illustration leaves little doubt that it is an example of *R. inequicostatus*.

The affinities of *'Pectinites' articulatus* SCHLOTHEIM and subsequent references thereto are discussed under *Ch. (Ch.) textoria*. Should it turn out that SCHLOTHEIM's type material is in fact representative of the species described in Section 3 an application to the ICZN for suppression of *'Pe.' articulatus* might be considered in the interests of stable nomenclature.



Text fig. 211: *Radulopecten inequicostatus* – frequency distribution for number of plicae on left valve.

Two specimens from the 'Rauracien Inférieur' of the Swiss Jura (DE LORIOL, 1894) constitute the only certain records from the L. Oxfordian but *R. inequicostatus* is locally abundant in the M. and U. Oxfordian (see Section 7).

Certain Kimmeridgian records are restricted to the eastern Jura (DE LORIOL, 1881) and to the southern and eastern parts of the Paris Basin (MNP; DECHASEAUX, 1936). *R. inequicostatus* is recorded from the Oxfordian/Kimmeridgian of Haute Marne (DE LORIOL et al., 1872), Charente Maritime (COQUAND, 1860) and Poland (SIEMIRADZKI, 1893).

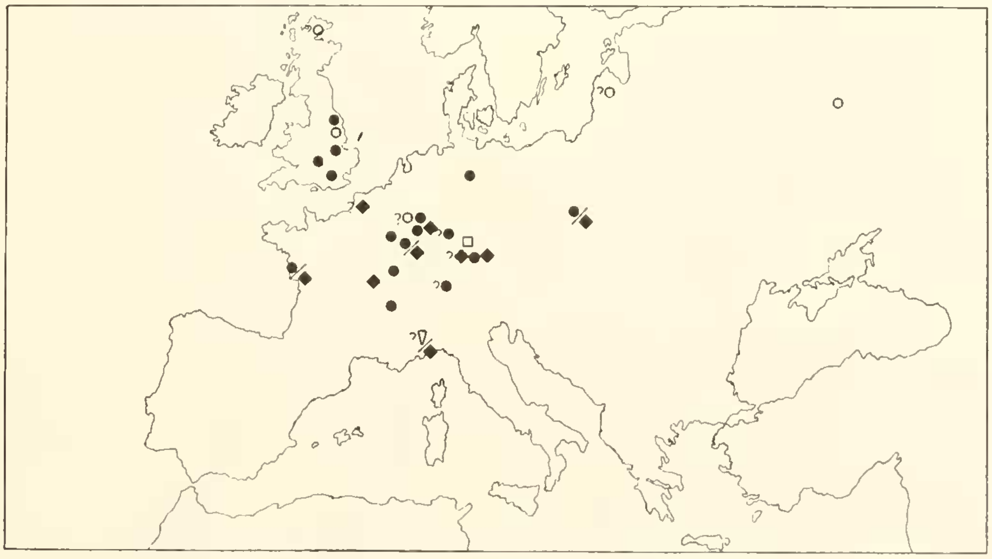
There are no certain records of *R. inequicostatus* after the Kimmeridgian. A Tithonian specimen referred to *'P.' ('Aequipecten')* cf. *inaequicostatus* PHILLIPS by KILIAN and GUÉBHARD (1905) is discussed in Section 4.

5. STRATIGRAPHIC RANGE

Four specimens (GPIT; Pl. 11, Fig. 2) from the Great Oolite (Bathonian) constitute the earliest records of *R. inequicostatus*. Certain Callovian records are restricted to two rather poorly preserved specimens (YM 592f, BM L21817) from the U. Cornbrash of Yorkshire. BRIGHTON (pers. comm. in COX and ARKELL, 1948: 13) has shown that LYCETT's (1863) figured specimen of *'P.' inaequicostatus* PHILLIPS, supposedly from the U. Cornbrash of Yorkshire, is in fact derived from the Oxfordian. Doubtfully conspecific specimens from the Callovian either referred to or compared with species which are synonymous with *R. inequicostatus* are discussed in Section 4.

6. GEOGRAPHIC RANGE

Within Europe (text fig. 212) common occurrences of *R. inequicostatus* are strongly correlated with the development of coral reef facies (see Section 7). However, within such facies there appears to be a northward diminution in numbers, probably due to a temperature restriction. Compared with its abundance in reef facies in France and Switzerland *R. inequicostatus* is rare in reefal and peri-reefal sediments in Yorkshire. Only 12 museum specimens (YM 204, 559[2]; BM 23173, 23347, 23359, 23363, 47148[2]; SbM P141, P149; SM) are known and intensive field work by the author has brought to light only two more somewhat questionable examples.



Text fig. 212: *Radulopecten inequicostatus* – European distribution.

Text fig. 213: *Radulopecten inequicostatus* – World distribution (Callovian reconstruction).

To the south of Europe (text fig. 213) *R. inequicostatus* is known as far away as E. Africa (Cox, 1935a, 1965) and to the east it may extend to Japan (see Section 4).

7. DESCRIPTION OF ECOLOGY

R. inequicostatus is reported (Peron, 1905) to be the most abundant pectinid in the Oxfordian of the Yonne region and to be entirely restricted to the coral reef facies, where it reaches a maximum height of 75 mm (MNP). The associated fauna is described on p. 88. The species is likewise common (reaching a maximum height of 65 mm) in the Oxfordian coral reef facies in the Swiss Jura (de Loriol, 1893) and the coral-rich U. Oxfordian sediments of Meurthe and Moselle have also yielded numerous specimens (NM; H_{max}: 54). *R. inequicostatus* is not known to be common elsewhere in the Oxfordian but with the exception of solitary specimens cited by de Loriol (1895) and Cox (1935a) all records (text figs. 212, 213) are associated with corals, or coral-dwelling, or facultatively coral-dwelling pectinids (see p. 88). Most, if not all, of the Kimmeridgian and Oxfordian/Kimmeridgian records (see Section 5) are similarly associated.

8. INTERPRETATION OF ECOLOGY

It is clear from Section 7 that for at least part of its life history *R. inequicostatus* was heavily reliant on corals in some way. The absence of the species from apparently suitable coral-rich sediments in the L. Kimmeridgian of Montbéliard (Contejean, 1859) is at present inexplicable.

There is no evidence of competition with *Chlamys (Ch.) textoria*, a species which in reefs probably occupied the same microhabitats as at least juveniles of *R. inequicostatus* (see Section 9).

9. FUNCTIONAL MORPHOLOGY

Like the *Spondylopecten* species with which it usually occurs, *R. inequicostatus* has a thick and relatively convex shell, thus the 'wedged' mode of life suggested for the former group might be inferred for the latter species. However, the lack of plical lamellae on the right valve argues against such a conclusion and suggests a more conventional mode of life with only the right valve ever in contact with the substrate. The presence of a byssal notch indicates that the species was byssate, at least when young, and the association with corals implies that the latter provided the attachment surface. Adults may have been forced to recline by virtue of their large size and thick shells.

The irregular ornament, high convexity and thick shell of *R. inequicostatus* would have greatly hindered swimming and in spite of ontogenetic increase in the umbonal angle it seems likely that adult animals were essentially sessile. The high convexity and thick shell probably facilitated a 'siege' policy against predators.

10. ORIGINS AND EVOLUTION

R. inequicostatus undoubtedly evolved from *R. vagans*. Evolution of a form with a relatively invariant number of initial plicae, consistently developed early in ontogeny, and with consistently widely spaced plical lamellae and rare intercalary plicae, is apparently a case of 'genetic assimilation' (Waddington, 1957) and as such implies regulatory change. Other morphological changes (see Section 3) may imply evolution of the structural genome.

There are apparently no phyletic changes in *R. inequicostatus*. Maximum height in the Kimmeridgian (41 mm; MNP) is considerably less than in the Oxfordian (75 mm) but this is probably a reflection of the restricted sample (see Section 5) rather than an evolutionary reduction in size.

The paucity of Callovian records of *R. inequicostatus* is probably due to the scarcity of coralliferous facies in Europe at this time. However, there is no scarcity of coralliferous facies to account for the apparent extinction of the species in the Tithonian. A deterministic explanation for the demise of *R. inequicostatus* is as yet unavailable.

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APPENDIX I

Species described from the European Jurassic but not discussed in the systematic section of this work (see p. 17)

Pecten Insularum D'ORBIGNY 1850
P. nudus BUVIGNIER 1852
P. Kralikii CONTEJEAN 1859
P. Jarnacensis COQUAND 1860
P. delessei ÉTALLON in THURMANN and ÉTALLON 1862
P. pauciplicatus SCHLÖNBACH 1863
P. mica DUMORTIER 1869
P. Stoliczkai GEMMELLARO 1874
P. acrorysus GEMMELLARO and DI BLASI 1874
P. billiemensis GEMMELLARO and DI BLASI 1874
P. diplopsides GEMMELLARO and DI BLASI 1874
P. grammoprotticus GEMMELLARO and DI BLASI 1874
P. nebrodensis GEMMELLARO and DI BLASI 1874
P. oppeli GEMMELLARO and DI BLASI 1874
P. polyzonites GEMMELLARO and DI BLASI 1874
P. siculus GEMMELLARO and DI BLASI 1874
P. zitteli GEMMELLARO and DI BLASI 1874
P. (Amusium) cryptozonus GEMMELLARO and DI BLASI in GEMMELLARO 1878
P. (A.) megalotus GEMMELLARO and DI BLASI in GEMMELLARO 1878
P. clare rugatus BOEHM 1883
P. fraudator BOEHM 1883
P. spitzbergensis LUNDGREN 1883
P. indisus DE GREGORIO 1886b
P. permitinus DE GREGORIO 1886b
P. supradubius DE GREGORIO 1886b
P. leucus DE GREGORIO 1886d
P. Zwingensis DE LORIOL 1895
Chlamys meriani GREPPIN 1899
Ch. peticlerci GREPPIN 1899
P. lima FUCINI 1906
Ch. janiroides COSSMANN 1907a
P. polycyclus BLASCHKE 1911
P. (Entolium) Beneckei ROLLIER 1911
P. (Neithea ?) Rollieri COSSMANN 1916
P. Nalivinki BORISSIAK and IVANOFF 1917
P. Borissiaki KHUDYAEV 1928

APPENDIX II

Derivation of I_{50} Values

The moment of inertia ($I\,[\lambda_{/2}]$) for a half wavelength of any given sinusoidal corrugation can be calculated using the following formula from TIMOSHENKO and WOINOWSKY-KRIEGER (1959): –

$$I\,[\lambda_{/2}] = \frac{f^2h}{2}\left[1 - \frac{0.81}{1+2.5\left(\frac{f}{2l}\right)^2}\right]$$

Where f = amplitude (in mm.)
h = thickness of material (in mm.)
l = $\frac{\lambda}{2}$ (in mm.)

Multiplication by $\frac{100}{\lambda}$ yields a value for a 50 mm length of corrugated section (I_{50}).

In text fig. 8 the author has resolved into lines of equal I_{50} the results of calculations within the ranges: amplitude 0–5 mm, wavelength 1–40 mm, thickness of material 0.1–5 mm.